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Towards a climate-resilient conservation network in Portugal

Miguel B. Araújo [a,b,c,*], Diogo Alagador [b], Babak Naimi [b,d], Dora Neto [b], Alejandro Rozenfeld [b]

[a] Department of Biogeography and Global Change, National Museum of Natural Sciences, Consejo Superior de Investigaciones Científicas (CSIC), Calle Jose Gutierrez Abascal, 2, 28006 Madrid, Spain
[b] Rui Nabeiro" Biodiversity Chair, MED – Mediterranean Institute for Agriculture, Environment and Development & CHANGE – Global Change and Sustainability Institute, Universidade de Évora, Largo dos Colegiais, 7004-516 Évora, Portugal
[c] Theoretical Sciences Visiting Program, Okinawa Institute of Science and Technology Graduate University, Onna, 904-0495, Japan
[d] Quantitative Biodiversity Dynamics (QBD), Department of Biology, University of Utrecht, Padualaan 8, Utrecht, 3584, CH, the Netherlands

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ABSTRACT

In response to the European Biodiversity Strategy 2030, Portugal is updating its conservation plans to expand the coverage of existing conservation areas from 22 % to 30 %. This expansion is also required to accommodate biodiversity adaptation needs amid climate change. To this end, we have developed a protocol that employs biological data, species distribution models, and optimization techniques within a systematic conservation planning framework, to guide the expansion of conservation areas while considering the needs of species adaptation under climate change. The protocol formulates scenarios considering three species' conservation targets and two climate scenarios. It identifies potential range retention refugia, where species may continue to persist, and range displacement refugia, where species might be forced to redistribute due to changing climatic conditions. Using terrestrial vertebrates as a test case, two regions emerge as critical for species conservation through the 21st century: the central-western region along the Atlantic coast, projected as future displacement refugia, and the northeastern upland region, serving both as range retention and displacement refugia. Additional smaller areas are identified mainly across mountains and coastal areas of the country. Importantly, existing conservation areas already encompass high concentrations of species in range retention refugia, preserving nearly double the species richness found in non-conserved areas. The proposed approach ensures that conservation expansion is both scientifically sound and effectively contributes to the biodiversity goals of 2030, representing a significant improvement over traditional approaches that rely on bottom-up expert judgment and administrative expediency.

1. Introduction

European member states are undergoing revisions of their conservation plans to meet the ambitious targets of the European Commission (EC) in its May 2020 release of the EU Biodiversity Strategy 2030 (EC, 2020). Among the targets, Portugal will need to increase its conservation area network from the current 22 % to 30 %, with a significant uplift in strictly protected areas from merely 0.02 % to 10 %. Moreover, European member states are requested to consider the expansion of conservation areas within the context of both mitigating climate change and adapting to its impacts.

In Portugal, the identification and classification of nationally-designated protected areas have traditionally been guided by a mix of bottom up and top down evaluations of sites' conservation values (Araújo, 1999; Araújo et al., 2007). The bottom-up approach—often referred to as the opportunistic selection process in the early conservation planning literature (Pressey et al., 1993)—has evolved through the gradual incorporation of new areas, driven partly by the accumulating insights into their natural value and partly by emergent opportunities for network expansion. In marked contrast, the establishment of the European Natura 2000 network was identified through a comprehensive top-down methodology. This process was characterized by the early establishment of specific criteria for species and habitats requiring preservation, meticulous analysis of the distribution and conservation status of these prioritized elements at a biogeographical level, and thorough engagement with regional stakeholder's integral to the decision-making

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* Corresponding author at: Departmento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC),Calle Jose Gutierrez Abascal 2, 28006 Madrid, Spain.
E-mail address: maraujo@mncn.csic.es (M.B. Araújo).

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framework.

While the EU Biodiversity Strategy 2030 does not prescribe more than general guidelines for the revision and expansion of conservation areas (EC, 2022), the present context—marked by an abundance of high-resolution, spatially explicit biodiversity data (e.g., Devictor and Bensaude-Vincent, 2016), significant advancements in the scientific and technological foundations of spatial conservation prioritization (e.g., Kukkala and Moilanen, 2013), and the complex optimization challenges posed by the need to incorporate climate change considerations (e.g., Jones et al., 2016)—as extensively described for Europe (Araújo et al., 2011)—demands systematic conservation planning approaches. The necessity for robust, replicable, and transparent scientific guidance in participatory processes (e.g., Fagerholm et al., 2021) reinforces the need for such approaches, as they promote accountability and ensure the effectiveness of conservation efforts. The systematic conservation planning approach is thus essential for identifying and integrating new areas into existing conservation networks, ensuring that expansion efforts are grounded in rigorous scientific rationale and participatory inclusivity.

To tackle the challenges associated with expanding conservation areas in Portugal, we have devised a protocol for guiding the identification of new areas to be integrated into the existing conservation network, which currently includes the nationally designated protected areas ("Rede Nacional de Áreas Classificadas", RNAP) and the European-wide Natura 2000 network (Special Areas of Conservation, SAC, under the Habitat Directive, and Special Protection Areas, SPA, under the Birds Directive). Together these areas constitute the National System of Classified Areas ("Sistema Nacional de Áreas Classificadas", SNAC). The conservation area selection protocol was designed with an emphasis on achieving the long-term persistence of species (e.g., Cowling, 1999; Williams and Araújo, 2002), specifically recognizing the need to adapt conservation strategies in response to shifting climate conditions (e.g., Araújo et al., 2004; Hannah et al., 2007; Groves et al., 2012). The core of the approach lies in data-driven decision making, integrating species distribution models (e.g., Araújo and Williams, 2000; Carvalho et al., 2011) with spatiotemporal complementarity-based conservation prioritization algorithms that account for shifting species ranges under climate change (e.g., Williams et al., 2005; Phillips et al., 2008; Graham et al., 2010; Alagador et al., 2016), to generate expansion scenarios for conservation areas.

The conservation area priority scenarios proposed herein varied according to three predetermined conservation targets for each species, and two climate change scenarios. Specifically, we identified range retention refugia, where species can persist despite the impacts of climate change, and dispersal pathways that enable species to track changing climatic conditions (Araújo, 2009a). While several studies have addressed climate change effects on conservation priorities (e.g., Jones et al., 2016; Haight and Hammill, 2020; Stralberg et al., 2020), only a few have framed their assessments with methodologies explicitly seeking to optimize species representation within conservation areas while accounting for their adaptation needs under climate change scenarios. Furthermore, although some studies have addressed spatial conservation priorities in the context of climate change on the Iberian Peninsula, they have typically focused on specific taxa, such as herptiles (Carvalho et al., 2011), birds (Triviño et al., 2018), mussels and fish (da Silva et al., 2024). These studies have used spatial conservation prioritization software such as Zonation (Moilanen, 2007) or Marxan (Ball et al., 2009), which lack specific functions for addressing the challenges of prioritizing areas for species experiencing redistribution dynamics due to climate change (as exemplified by Williams et al., 2005; Phillips et al., 2008; Graham et al., 2010; Alagador et al., 2016). Our study is a pioneering effort in explicitly incorporating both spatial and temporal dimensions to calculate functional connectivity-the ease with which target species might move from place to place-while optimizing spatiotemporal conservation priorities for hundreds of species across multiple taxa. Our approach offers a spatial conservation planning protocol specifically designed to address the challenges of climate change. Furthermore, it has applicability beyond Portugal, providing a framework that can be adapted to any region where sufficient species distribution data are available to support the modeling and optimization tools developed.

2. Data and Methods

2.1. Species data

To align with the adopted protocol for modeling species distributions (see below), distribution data were originally compiled at the scale of the Iberian Peninsula for four taxonomic groups considered to have sufficiently robust data for modeling. These groups included mammals ($N = 61$; Minimum Number of Records = 45, Median = 814, Max = 5016), birds ($N = 171$; Minimum = 17, Median = 2131, Max = 5813), amphibians ($N = 27$; Min = 23, Median = 808, Max = 4738), and reptiles ($N = 33$; Min = 19, Median = 566, Max = 3755). In total, occurrence records for 292 terrestrial vertebrate species were mapped onto the 5928 10 km × 10 km UTM (Universal Transverse Mercator) grid. While it would have been desirable to include invertebrate and plant data, these data were unavailable at the time this study was conducted.

The compiled database was created by integrating extensively curated biological records across the Iberian Peninsula collected between the end of the 20th century and beginning of the 21st century, and previously used in a government-sponsored report on biodiversity conservation for the 2030 horizon (Araújo et al., 2022). The primary sources were the Institute for Nature Conservation and Forests (ICNF) in Portugal, which provides much of the data through an online repository (https://geocatalogo.icnf.pt/catalogo.html), and Spain's "National Inventory of Biodiversity" from the General Directorate of Natural Environment and Forest Policy, which also provides most of it data through an online data repository (https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/bdn-ieet-default.html). Additionally, for Portugal, we also used data from the Atlas of Mammals of Portugal (Bencatel et al., 2017).

These datasets were generated through state-sponsored or citizen- and academic-led initiatives aimed at characterizing species distributions on a standardized grid. Although sampling protocols varied among taxonomic groups—for instance, birds are surveyed more extensively than other groups (e.g., Tiago et al., 2017; Hughes et al., 2021; Taheri et al., 2021)—the vertebrate distribution data for Spain and Portugal are widely used to support research, environmental impact assessments, and public policy. These datasets are generally considered more reflective of the actual presence and absence of organisms than of the presence or absence of recorders.

Iberian species found outside Portugal's administrative limits were excluded from the modeling, as the focus of the study was on the conservation of species currently present within the country. The final database comprised 236 vertebrate species, including 44 mammals (Minimum Number of Records = 184, Median = 1598, Max = 5016, 150 birds (Min = 65, Median = 2528, Max = 5813), 18 amphibians (Min = 342, Median = 1179, Max = 4738) and 24 reptiles (Min = 57, Median = 965, Max = 3755) (Fig. S1A).

2.2. Climate data

Climatic data for the Iberian Peninsula were obtained from the WorldClim database (version 1.4; Hijmans et al., 2005), adopting and deriving the following variables: annual mean of minimum temperature (°C), annual mean of maximum temperature (°C), and annual mean of total precipitation (mm). For the reference period (1960–1990 averages), such data were obtained at a resolution of 5 arc-minutes (~81 km2) and 30 arc-seconds (~1 km2, https://www.worldclim.org/dat a/v1.4/worldclim14.html).

Future projections of the same variables (https://www.worldclim.org/data/v1.4/cmip5.html), at a resolution of approximately 1 km^2, were compiled for the year 2050 (2041–2060 averages) and 2070 (2061–2080 averages), according to two scenarios of greenhouse gas emission evolution, named Representative Concentration Pathways (RCP). Specifically, we chose to focus on RCP 6.0, which aligns with moderate mitigation efforts and assumes emissions will peak around 2080, reflecting current geopolitical uncertainties and delays in implementing strong climate policies. In contrast, the more extreme RCP 8.5 is considered by some authors to be more likely (Schwalm et al., 2020), representing continuous increases in greenhouse gas emissions throughout the 21st century, driven by the ongoing reliance on fossil fuels. It is important to note that the exact carbon emission trajectories are not fully established. While global efforts to mitigate emissions could moderate the trajectory, factors such as methane emissions from melting permafrost could exacerbate it. These uncertainties make it difficult to predict with certainty whether emissions will follow a more moderate path like RCP 6.0 or approach the more extreme RCP 8.5 scenario. By including both scenarios, we aim to capture a range of possible futures, accounting for uncertainties in future economic trends and policy decisions. These climate change projections derive from ten models produced in the fifth phase of the Coupled Model Intercomparison Project Phase 5 (CMIP5), considered in the context of the fifth report (AR5) of the Intergovernmental Panel on Climate Change (IPCC). Namely: BCC-CSM1–1, CCSM4, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, MIROC5, MRI-CGCM3, and NorESM1-M.

2.3. *Species distributions models*

When examining species' potential responses to climate change, it is important to assess the relationship between species distribution and climate across a representative sample of their geographical distribution. Failing to do so may result in an overestimation of species' sensitivity to climate changes (e.g., Pearson et al., 2004; Thuiller et al., 2004). Therefore, to estimate species' potential responses to climate change in mainland Portugal, we developed models across the entire Iberian Peninsula (Fig. S1B). Models were fitted using the sdm package (Naimi and Araújo, 2016), implemented in R environment (R Development Core Team, 2021; version 4.1.1) and adopting the program's standard definitions (see also Naimi et al., 2022). Potential distributions of species were predicted for the reference period (1960–1980), then projected for two periods in the future (2041–2060 and 2061–2080) and across two emissions scenarios.

While the data originates from extensive national inventories of species' presence and absence, for support of conservation policies, the certainty of absence data varies across groups. Due to lack of detailed information about sampling intensity and to standardize the statistical assumptions across different modeling techniques—each of which handles absence (or zero) data differently, we opted to treat the data as presence-only. The conceptual distinction between treating data as presence-absence versus presence-only lies in how absence data contributes to information content. When treating data as presence-absence, true absence records are considered informative. In contrast, presence-only approaches use randomly generated pseudo-absence data as a background reference, leveraging presence data as the primary source of information. To implement the procedure for selecting background points, we randomly generated 1000 pseudo-absence (as "background") records (see also Steen et al., 2024) for each species across the Iberian Peninsula. This approach ensured consistency across models and minimized potential biases that could arise from varying interpretations of absence data by different algorithms.

For each species, we trained 11 statistical and machine learning algorithms: Generalized Linear Models (GLM) (McCullagh and Nelder, 1989), Generalized Additive Models (GAM) (Wood and Augustin, 2002), Classification and Regression Trees (CART) (Breiman et al., 1984), Boosted Regression Trees (BRT) (Elith et al., 2008), Random Forests (RF) (Breiman, 2001), Multiple Discriminant Analysis (MDA) (Hastie et al., 1994), Support Vector Machine (SVM) (Vapnik, 1997), Multivariate Adaptive Regression Spline (MARS) (Friedman, 1991), Maximum Entropy (Maxent) (Phillips et al., 2006), Domain (Carpenter et al., 1993), and Bioclimatic envelope (Busby, 1991). For each species and model, the *k*-fold cross-validation technique was used ($k = 5$) (James et al., 2013) where records were randomly assigned ("without replacement") to 5 groups each with 20 % of data. This means that the training for each modeling method was repeated 5 times using four groups (80 % of records) and evaluated using one of the groups (20 % of the data). Overall, 55 distribution models were adjusted for each species (11 methods × 5 cross-validation replications). We acknowledge that randomly partitioning the data into training and test sets does not ensure independence between them (Araújo et al., 2005a). As such, model evaluation under this approach is better regarded as an internal validation—or verification—of model fit, rather than an external assessment of predictive performance (Oreskes et al., 1994; Araújo and Guisan, 2006).

Internal assessment of the models' performance was based on three metrics: the ROC Curve ("Receiver Operating Characteristic") and the AUC ("Area Under the Curve") metric (Swets, 1988), the TSS ("True Skill Statistic") (Allouche et al., 2006), and the CBI ("Continuous Boyce Index") (Boyce et al., 2002; Hirzel et al., 2006). When using presence-only data, AUC and TSS metrics should be interpreted with caution due to the unknown prevalence of species. However, since our data is reasonably interpreted as presence-absence and the background sampling strategy adopted preserves the original ranks of prevalence, these two metrics were considered appropriate indicators of performance. AUC values range from 0 to 1, with values below 0.5 indicating worse-than-chance discrimination, 0.5 representing random discrimination, and 1 indicating perfect discrimination. TSS, calculated as "sensitivity + specificity - 1" and ranging from −1 to +1, similarly serves as a performance measure, with values closer to +1 indicating stronger predictive agreement. Finally, CBI measures the ratio of predicted presences to expected presences, based on the continuous habitat suitability generated by the model, providing insight into model calibration. This approach is 'blind' to absence data, hence being generally preferred for evaluation outputs of presence-only SDMs trained with background records. A well-calibrated model will have a CBI close to 1, indicating that predicted probabilities closely reflect observed frequencies, 0 indicates random predictions, and negative values suggest predictions worse than random. The accuracy of species distribution maps resulted from the ensemble predictions (see next section) were assessed using the existing presence and absence records using AUC and TSS metrics. In addition, the presence-background records were used to estimate the accuracy using the CBI. The results of the models' evaluations are recorded in Supplementary Fig. S2 and Supplementary Table S1.

While model training and validation was conducted at the 10 × 10 km UTM grid, matching the resolution at which species data were sampled, predictions and projections were statistically downscaled to a 1 × 1 km grid, in line with the resolution of the climate data (Fig. S1B) (Araújo et al., 2005b).

2.4. *Ensembles*

For each species, we combined the outcomes of the different models to obtain a consensus within an ensemble forecasting framework (Araújo and New, 2007), an approach demonstrated through both model-data (Araújo et al., 2005c) and model-model comparisons (e.g., Marmion et al., 2009; Crimmins et al., 2013; Zhu and Peterson, 2017) to generally improve predictions and projections compared to the individual models that constitute them. Specifically, we estimated a consensus distribution among the 55 models for each species using the AUC-weighted mean across the models (e.g., Garcia et al., 2012; Naimi et al., 2022). The square of the weights was used to assign higher weights to better-performing models. Although there is no guarantee that best performing models in our test data would always perform best on an independent future under climate change, there is even less guarantee that clearly underperforming models in our test data would perform well in the future. The selected models were used to project the distribution of species into the future periods, and then the outcomes of different models were combined using the same approach, representing a weighted consensus species distribution model for different future scenarios. The resulting maps were reclassified into binary maps indicating the presence or absence of the species, using a threshold that maximized TSS (= maximized sum of sensitivity and specificity) for each species (e.g., Liu et al., 2005).

2.5. *Functional connectivity and area prioritization*

Our conservation prioritization protocol is based on the principle of complementarity, which seeks to identify the optimal combination of areas that maximize biodiversity representation, as first proposed by Vane-Wright et al. (1991). Building on the foundational work of Williams et al. (2005), we developed a protocol for selecting complementary sets of viable conservation under climate change. The protocol advances over traditional complementarity-based spatial conservation planning by identifying sets of areas that optimize expected occurrence across both spatial and temporal dimensions. Two key biogeographical concepts underpin this approach: climate change retention refugia, where species are expected to persist within their current ranges despite climate change, and displacement refugia, where species are anticipated to migrate to new areas in order to survive (Araújo, 2009a; also termed "in situ" and "ex situ" refugia, respectively, Brambilla et al., 2022) (Fig. 1).

Formally, retention refugia are defined as areas (or grid cells on a map) where a species' presence remains consistent across n designated time periods (in this study, $n = 3$). These periods include an initial time point when the species was recorded ($t0$), and two subsequent time points ($t1$ and $t2$) where the species is projected to persist. Retention refugia thus represent stable conditions where the climate remains suitable for the species over time, making them areas of high conservation value that should be prioritized to ensure the species' long-term survival.

In contrast, displacement refugia are areas where a species is initially absent in $t0$ but where multiple species are expected to converge as they track shifting climate through dispersal. These areas identify future habitats essential for accommodating species displaced by climate change, serving as critical targets for conservation planning.

While these two biogeographical concepts are critical for understanding the dynamics driving changes in spatial prioritization, the operational concept used to implement spatiotemporal complementarity optimization is the related concept of dispersal chains (Williams et al., 2005; Phillips et al., 2008). Dispersal chains are sequences of grid cells that enable species to track climate changes, optimized to minimize traveled distances and thereby increase the likelihood of successful species movement over time.

Unlike displacement refugia, dispersal chains are calculated from areas where the focal species is already present. However, both are affected by the direction and magnitude of climate change, the spatial patterns of displacement refugia and dispersal chains are expected to converge. Dispersal chains may sometimes overlap spatially, and chains consisting of a single cell (where species presences remain consistent over time) are considered to have zero spatiotemporal dimension and are formally classified as a retention refugia.

Given the three time periods considered in this study, dispersal chains with non-zero- dimension consist of three grid cells or, in cases where a single cell remains relevant across two periods, two grid cells. For the calculation of dispersal chains, we set a maximum connectivity distance of 100 km between grid cells in successive time periods. Although this distance is arbitrarily chosen and does not directly reflect the biological dispersal capacities of species over the period considered, it is essential for defining the range within which the algorithm searches for feasible dispersal routes.

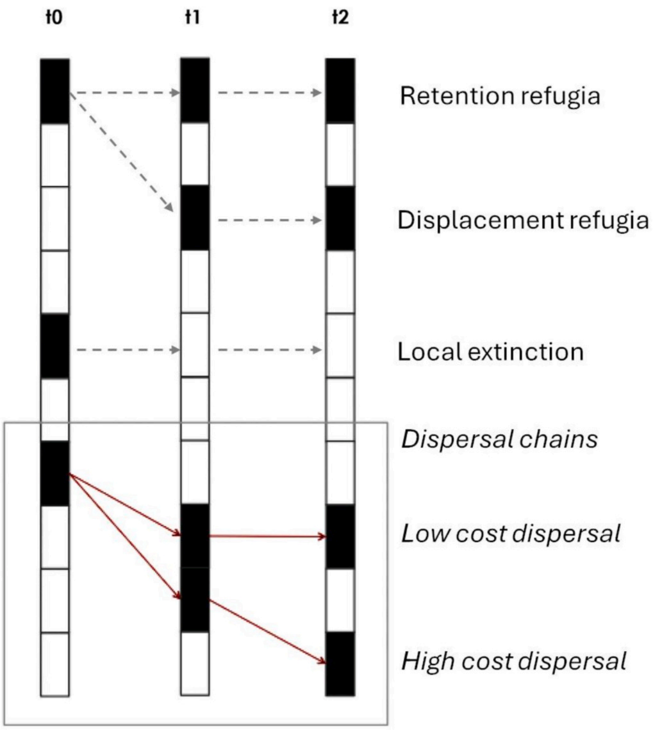


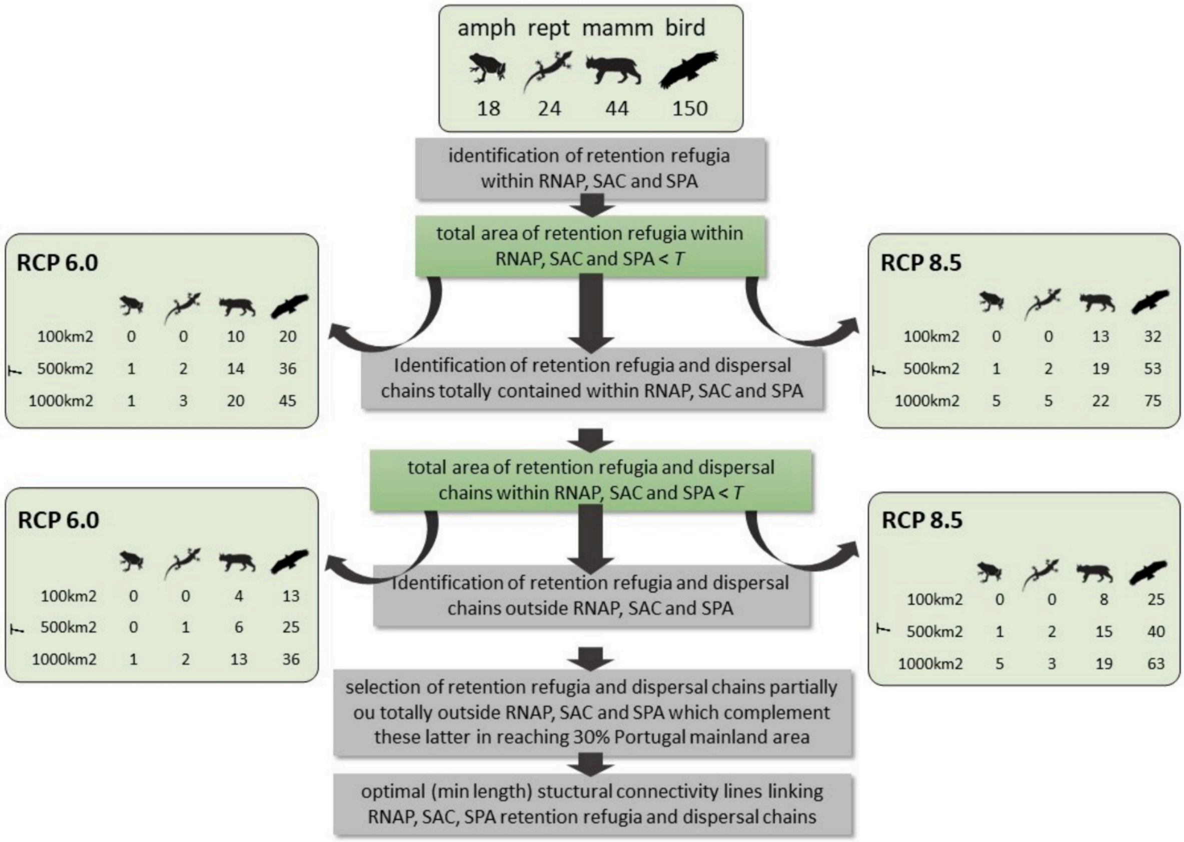
Fig. 1. One-dimensional schematic representation of climate change refugia and dispersal chain identification. Each column represents a map with 1 km grid cells for the reference time (t0), horizon 2050 (t1), and horizon 2070 (t2). Black indicates the presence of the species in a grid cell, and white indicates its absence. Dispersal chains are sets of grid cells (>1, ≤ 3) that allow for the persistence of species populations across the three climate horizons. In the case of a retention refugia, a single grid cell is sufficient to ensure the persistence of a species' population. In cases of forced dispersal, due to projected disappearance of local suitable climate conditions for a particular species, shorter dispersal chains are favored as they offer a lower "cost" of movement for the species. Areas with a high concentration of dispersal chains constitute displacement refugia.

The process of identifying dispersal chains and retention refugia—the latter being a dispersal chains with zero spatiotemporal dimension—requires distinct analytical approaches. Since species persistence is more probable within climate change retention refugia, these areas are prioritized over non-zero-dimensional dispersal chains, where the risks and uncertainties associated with movement through the landscape increase with dispersal distance. The analysis of retention refugia is relatively straightforward, involving a local comparison of species occurrences by overlaying maps across three time periods. Specifically, we identify retention refugia as locations where species are observed in 10 km grid cells under current conditions, and where models predict and project their continued presence in the future within the nested 1 km cells of those same 10 km units.

In contrast, the identification of non-zero dispersal chains employ more complex principles of graph theory. This mathematical framework models relationships and pathways within a set of nodes (cells), connected by edges (distances), which represent the movement potential, or functional connectivity, between these points. For dispersal chains, the graphs constructed for each species consist of three sequential sets of nodes, where each set corresponds to the grid cells representing the observed species occurrences (at time $t0$) or the projected occurrences (at times $t1$ and $t2$). Edges within this graph connect pairs of nodes across these sequential sets, but only if the grid cells they represent are within the predetermined dispersal distance—defined here as 100 km or less. These connections are not simply binary; each edge is assigned a value that reflects the geographical distance between the grid cells it links.

For each species ($n = 236$), and climate scenario (RCP 6.0 and RCP 8.5), we identified a given number of retention refugia and independent dispersal chains, depending on the conservation targets (see below). A set of chains is qualified as independent if no chains overlap in the same grid cell in any period. This independence is crucial for accurately assessing species' representation over time, aligning with conservation targets. Notice that the greater the number of independent chains per species the greater the likelihood of identifying shared chains among multiple species, making area conservation optimization more cost-efficient (Williams et al., 2005). However, managing chain independence is computationally intensive, requiring significant resources and processing time due to its mathematical complexity and fine spatial resolution involved. To maximize the expected persistence of species in these chains, we prioritized chains minimizing dispersal distances, employing the optimal algorithm (developed by De Queirós Vieira Martins et al., 1999), adjusted to ensure chain independence (Alagador et al., 2016). The protocol for implementation of our methodology unfolds as follows:

1. Definition of representation targets (T): Establish specific conservation targets for each species, determining the minimum coverage to be consistently maintained across the three periods of time considered in the analysis (T1 = 100 km^2, T2 = 500 km^2, or T3 = 1000 km^2). The 100 km^2 target aligns with the rarity threshold for identifying critically endangered species under the IUCN Red List (see also Williams et al., 2005). The higher targets (500 km^2 and 1000 km^2) were included to explore more ambitious conservation scenarios, while remaining within the constraints of current policy goals—particularly the aim of protecting 30 % of the national territory.
2. Identification of species fully conserved in retention refugia: Species that meet the designated conservation target (T) within existing conservation areas and climate retention refugia (assessed by simple matching of focal species occurrences with these areas, Araújo, 2004)—where species persistence is predicted highest—are classified as adequately represented and protected.
3. Identification of dispersal chains required to meet targets T: For species that do not fully meet the conservation target due to a lack of suitable retention refugia within existing conservation areas, dispersal chains that are fully covered by existing conservation areas are examined.
4. Refugia and chains in unclassified areas: If the area of climate retention refugia and dispersion chains for a given species does not meet the conservation target (T) within existing conservation areas, the process is repeated in unclassified areas. This step identifies additional refugia and chains necessary to meet conservation targets, focusing on minimizing representation deficits in classified areas.
5. Minimizing underrepresentation: For species with an insufficient representation within refugia and chains, all areas identified in step 4 are designated as necessary to minimize underrepresentation relative to the conservation target (T). This ensures that all species are



RCP 6.0

100km2	0	0	10	20
500km2	1	2	14	36
1000km2	1	3	20	45

RCP 8.5

100km2	0	0	13	32
500km2	1	2	19	53
1000km2	5	5	22	75

RCP 6.0

100km2	0	0	4	13
500km2	0	1	6	25
1000km2	1	2	13	36

RCP 8.5

100km2	0	0	8	25
500km2	1	2	15	40
1000km2	5	3	19	63

Fig. 2. Structured protocol for the prioritization of conservation areas. The protocol seeks to complement existing conservation areas to meet the 30 % conservation area target, while accounting for the adaptation needs of species response to climate change. Three individual species area targets are set (T = 100 km2, 500 km2, and 1000 km2) under two future climate scenarios (RCP 6.0 and RCP 8.5). Embedded tables display the number of species in each taxonomic group (amphibians, reptiles, mammals, and birds) that do not meet the representation target in retention refugia, and dispersal chains located within the nationally designated protected areas and Natura 2000, hence necessitating additional conservation areas across non-conserved areas.

adequately represented in conservation planning, addressing gaps in classified areas.

6. Area optimization: The identification of new conservation areas typically follows an optimization procedure designed to minimize the additional area required, thereby maximizing efficiency. A greedy-type heuristic algorithm selects areas based on incremental species richness from the dispersal chains, ensuring that conservation efforts focus on the smallest possible area while meeting the conservation targets for all species. The process stops once the existing conservation areas and the selected refugia together reaches 30 % of the mainland of Portugal (Fig. 2). In our case, this final optimizing step was unnecessary because the retention refugia and dispersal chains identified in previous steps under the most stringent conservation targets, complemented the current conservation areas, achieving approximately 30 % coverage of mainland Portugal.

2.6. *Structural climate connectivity*

After identifying the optimized retention refugia and dispersal chains—which can be understood as the "natural blocks" from which structural connectivity is sought to promote movement between them (see framework of best practices for developing regional connectivity maps in Beier et al., 2011)—we developed a method to map climate connectivity between these areas. This method specifically focuses on spatially connecting conservation areas formally classified under the SNAC (including the RNAP, SAC, and SPA), along with climate retention refugia and dispersal chains. Structural climate connectivity begins with a zonation of microclimatic and topographic features that facilitate species movement across landscapes experiencing rising temperatures and increased aridity (the anticipated scenarios for the region; e.g., Dasari et al., 2014; Andrade et al., 2021; Carvalho et al., 2021). Unlike dispersal chains, structural connectivity corridors are not species-specific. Instead, they focus on identifying critical land facets—recurring landscape units with uniform topographic attributes—that are generally considered favorable to species dispersal (Beier and Brost, 2010). For this reason, they are also referred to as static elements of connectivity (Goicolea and Mateo-Sánchez, 2022). In our study, the climate connectivity corridors are designed to identify pathways between areas that minimize weighted distances, with weights determined by three relevant landscape features (see Fig. S3): topographic heterogeneity; slope orientation; and the presence of wet features (coastal and wetland).

Topographic heterogeneity was determined using a 25-m resolution digital terrain model (DEM) from EPIC WebGIS spatial infrastructure (http://epic-webgis-portugal.isa.ulisboa.pt/), capturing variation in elevation among adjacent grid cells. Areas with heterogeneity above the national median were considered relatively more favorable for connectivity (Fig. S3). This approach is based on understanding that regions with diverse topography exhibit greater microclimatic variability, allowing species to adapt to climate changes through short-distance movements (e.g., Game et al., 2011; Schloss et al., 2022). Indeed, analyses have shown that areas with low topographic diversity often require longer migrations for species to adjust to similar climatic shifts, while mountainous regions tend to experience the slowest rates of climate change (Peterson, 2003).

Slope orientation was derived from the same 25-m resolution DEM (Fig. S3). Slopes are associated with structural and enduring microclimatic factors, serving as proxies to the relationship between microclimate and geomorphology (e.g., Shreve, 1924; Seyfried et al., 2021). Given Portugal's position in the northern hemisphere and its proximity to the North Atlantic, north-facing (cooler) and west-facing (more humid) slopes have been identified as more favorable (Fonseca and Santos, 2018), while south-facing (warmer) and east-facing (drier) slopes were excluded for climate change connectivity. This is particularly relevant under the increasingly extreme summer temperatures observed across much of Portugal, especially in the southern and eastern regions, where thermal conditions often exceed the upper critical limits of many species, including thermally tolerant taxa such as reptiles (Araújo et al., 2013). While species may buffer such stress through behavioral strategies such as estivation or the use of shaded refuges (Sinervo et al., 2010; Herrando-Pérez et al., 2020), these options depend on habitat availability. In other words, all else being equal, areas offering greater shade and moisture—such as north- and west-facing slopes—are more likely to support species' vital activities, including foraging and dispersal, and are thus more appropriate for structural connectivity under climate change.

Coastal and wetland corridors as defined by the 'Direção-Geral do Território' (DGT) were also incorporated. Wetland corridors, mapped based on riparian zones from the LU/LC 2012 (Copernicus Land Monitoring Service; https://land.copernicus.eu/en/products/riparian-zones) with a minimum cartographic unit of 0.5 ha, are an initiative supported by the European Commission, the European Space Agency, and the European Environment Agency, in collaboration with member states. Coastal corridors cover the coastal zone extending 2000 m from the coastline, excluding areas characterized by impermeable surfaces such as built-up fabric, industry, commerce, agricultural facilities, transportation, inert extraction sites, waste deposition, and construction zones as outlined in the 2018 Land Use and Occupation Map (COS) produced by the DGT. Due to legal restrictions on development in these areas, they serve as vital green infrastructures promoting landscape connectivity.

By overlaying the three layers of information, we created a climate connectivity cost surface. Areas that meet all three criteria exhibit the highest connectivity (cost = 1), those meeting two criteria show intermediate connectivity (cost = 2), and areas meeting only one criterion have low connectivity (cost = 3). Regions that do not meet any of the criteria are deemed unsuitable for climate connectivity (Fig. 3).

Following the estimation of the cost surface, we developed efficient climate connectivity scenarios using the "Optimal Region Connections" tool in ArcGIS Pro 2.9.0 (ESRI, Redlands, CA, USA). The first scenario, termed "regionally optimized", establishes multiple paths between each node (nationally designated conservation areas and optimized climate refugia) and its nearest areas through a cost-allocation process that considers both Euclidean and cost distances. The second scenario, named "globally optimized", moves beyond the initial multiple paths (edges) and employs a graph theory algorithm to compute the minimum spanning tree. This approach identified the most cost-effective connectivity between the nodes by considering the cumulative costs (edges' weights). The regionally optimized scenario prioritizes local connectivity, emphasizing multiple pathways and resilience for biological network connectivity. While this scenario is generally more "expensive" in terms of overall cost, it provides flexibility and redundancy by offering various dispersal routes. In contrast, the globally optimized scenario focuses on global efficiency, generating fewer but more effective paths to optimize the overall network's connectivity.

3. Results

3.1. *Projected impacts of climate change on vertebrate species*

Climate change is expected to impact different groups of vertebrates examined in Portugal to varying degrees (Fig. 4). Seventy to 80 % of bird and mammal species are projected to lose portions of their potential distributional range, while amphibians (62 %–69 % of species) and reptiles (45 %–50 % of species) face somewhat less severe impacts. Specifically, birds and mammals are likely to see the most substantial range reductions, with median contractions of their potential distribution exceeding 78 %. In contrast, while amphibians and reptiles are projected to experience significant variability between climate scenarios, their median range losses are projected to be a little less drastic under RCP6.0 at 76 % for amphibians and 63 % for reptiles.

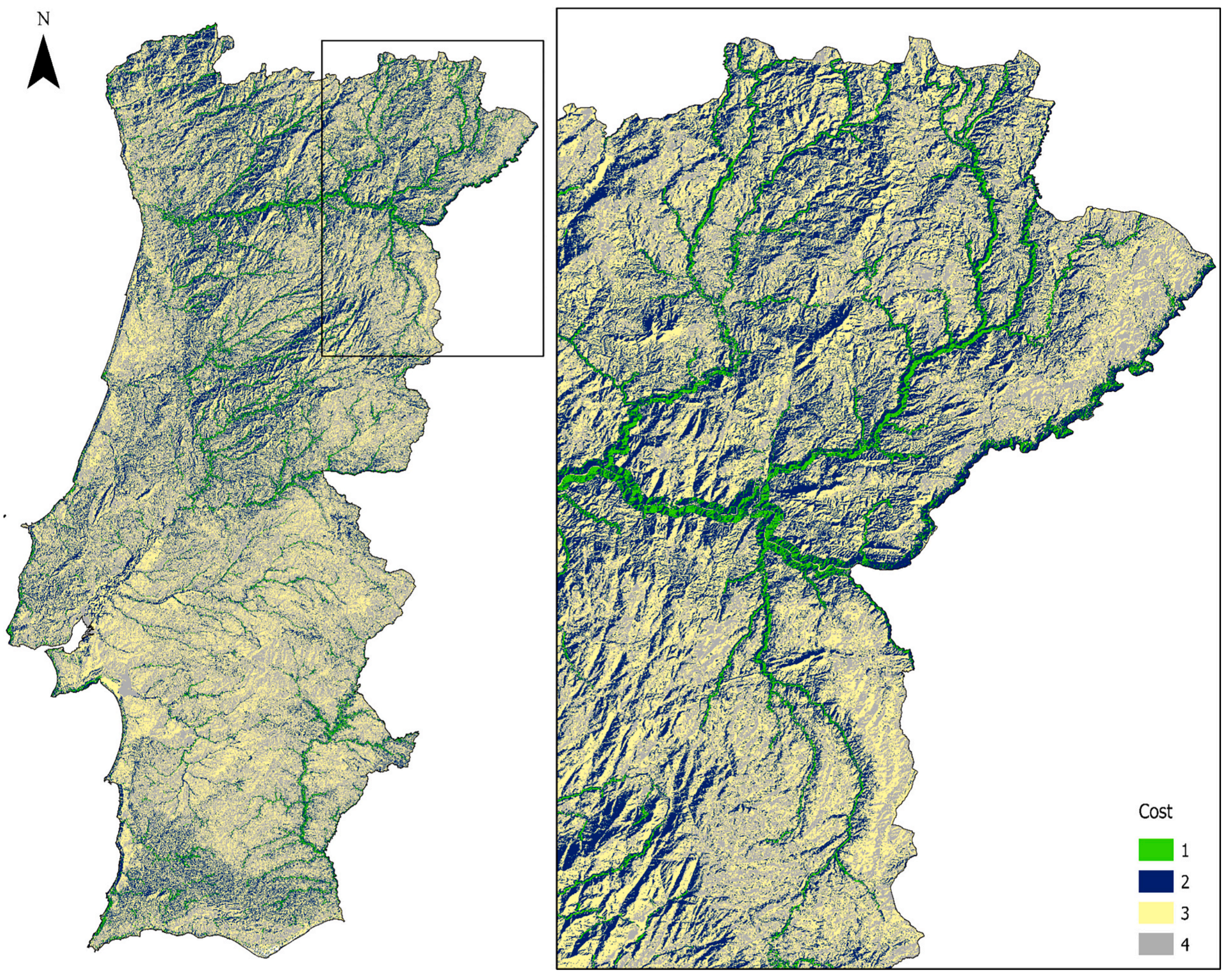


Fig. 3. Climate connectivity cost surface at a resolution of 25 m, organized in descending order from the most to the least favorable: 1) coastal/wetland corridor areas from the DGT with higher orographic variability (> 50th percentile of orographic heterogeneity) and the presence of north-facing (cooler) or west-facing (more humid) slopes; 2) areas with only two coinciding criteria, coastal/wetland corridors from the DGT with higher orographic variability (> 50th percentile), coastal/wetland corridors from the DGT with north or west-facing slopes, or north or west-facing slopes with higher orographic variability (> 50th percentile); 3) areas meeting only one of the criteria considered, coastal/wetland corridors from the DGT, higher orographic variability (> 50th percentile), or the presence of north or west-facing slopes; 4) areas without any of the considered criteria. The original data layers used to calculate the cost surface can be visualized in Fig. S3.

3.2. Retention and displacement refugia

When spatializing these climate suitability trajectories, distinct patterns in the distribution of range retention and range displacement refugia emerge (Fig. 5). In central Portugal, particularly in western coastal areas, and in the northeast, several amphibian species are expected to find both types of refugia, marking these regions as critical for their 21st century persistence. Reptiles, preferring warmer climates, predominantly find retention refugia in southern Portugal along the coast of Algarve although areas of complex orography in the central and northern parts of the country are also projected to be important. Their displacement refugia are widely distributed, extending from southern regions into the central west of the country. In contrast, mammals and birds primarily locate their retention refugia in the northeastern part of Portugal, an area that also hosts displacement refugia for these groups.

Two key regions emerge as critical for preserving climate patterns conducive to species adaptation through 2080: the central-west region along the Atlantic coast, known in Portugal as “Oeste” (West), which is projected to serve as future displacement refugia, and the northeastern region of “Trás os Montes”, projected to function both as range retention and displacement refugia for all groups considered (Figs. 5 and 6). The latter region benefits from moderate coverage by conservation areas, including RNAP and Natura 2000 sites (Fig. 6). However, the central west, lacking in conservation areas, is identified as a priority for urgent conservation efforts. Interestingly, there is no great difference in average species richness among the dispersal chains across the three types of conservation areas (Table 1). However, protected areas (RNAP sites) tend to encompass higher concentrations of species displaying a range retention refugia pattern than Natura 2000 sites (SAC and SPA sites), offering nearly double the species richness compared to unprotected areas (Table 1). This underscores the critical role of targeted conservation strategies in areas already protected under national and European law.

3.3. Distances and trajectories in dispersal chains

The distances species need to travel to track climate change from their currently conserved territories to other suitable habitats, via the calculated chains, vary significantly depending on the species group, RCP scenario, and the period assessed (Fig. 7). For amphibians under the RCP 6.0 scenario, the median distance from the baseline to 2050 is 44.5 km (range: 1–100 km), decreasing to 13.5 km (range: 1–100 km) between 2050 and 2070. In contrast, under the RCP 8.5 scenario, the median distance for amphibians is 10.1 km from the baseline to 2050 (range: 1–93 km), dropping sharply to 1.9 km (range: 1–98 km) in the period mediating 2050 and 2070. Reptiles exhibit a different pattern,

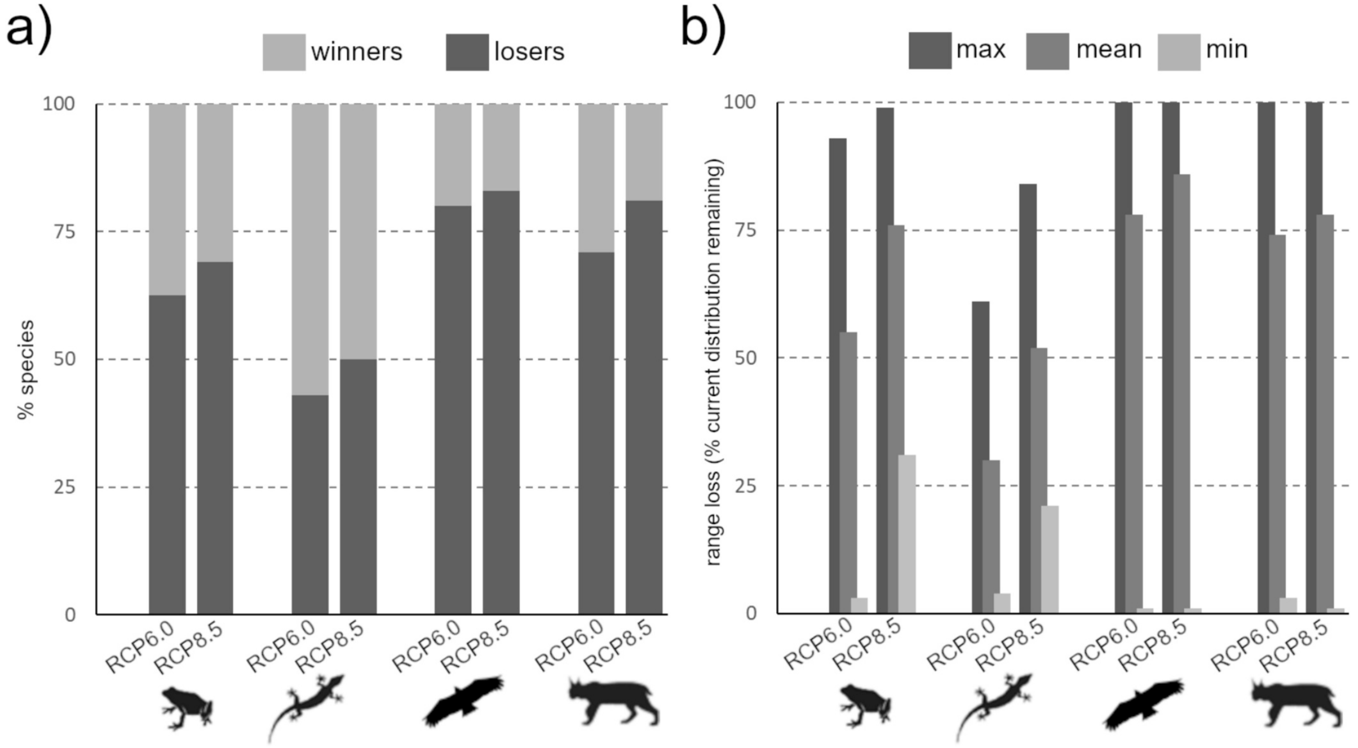


Fig. 4. Impacts of climate change on the modeled species potential distributions under two RCP scenarios. a) percentage of species in each taxonomic group that potentially gain and lose suitable climate; b) percentage of the current potential distribution area lost by the losing species (boxes define the 1st and 3rd quartiles, whiskers convey to inter-quantile ranges, vertical lines are median values, crosses are mean values and points are outliers).

with an average distance of 11.8 km (range: 1–73 km) under RCP 6.0 and 17.4 km (range: 1–100 km) under RCP 8.5 from the baseline to 2050. Between 2050 and 2070, reptile distances decrease significantly to 4.2 km (range: 1–57 km) under RCP 6.0 but increase to 23.1 km (range: 1–100 km) under RCP 8.5. Birds and mammals show more consistent tracking distances, requiring median distances of 17–46 km to track climate change from the baseline to 2050 under both RCP scenarios. From 2050 to 2070, birds need to move an average of 3.1 km (range: 1–100 km) under RCP 6.0 and 12.9 km (range: 1–100 km) under RCP 8.5, while mammals travel 2.9 km (range: 1–100 km) and 5.6 km (range: 1–100 km) under RCP 6.0 and RCP 8.5, respectively.

By documenting the expected number of species displaced from existing conservation areas due to shifting climate conditions and characterizing the projected number and direction of their chains, we can map the distributional flows originating from conservation areas to other conserved or non-conserved areas (Fig. 8). The geography of these dispersal chains reflects the topographic and physiographic features of mainland Portugal, often illustrating movements from lowlands to highlands or from inland areas towards the coast. Concurrent with the patterns described for Fig. 6, the west and northeast emerge as significant displacement refugia for species. Additionally, more subtle patterns are observed: southward movements from the Guadiana River Valley, which partially includes the corresponding Natural Park, towards the mountainous areas of the Algarve; upward movements, both eastward and southward, towards the mountains along the eastern border of Portugal with Spain, encompassing a section of the St. Mamede Natural Park; westward and southward movements towards the Natural Park of the Estrela Mountain in central north Portugal; northward displacement along the Coa Valley from the Natural Park of Malcata Mountain towards the Douro River; and westward movement from the northernmost region of Portugal towards the National Park of Gerês.

3.4. Climate-change resilient spatial conservation priorities

From our analysis of nationwide spatiotemporal biodiversity patterns, we have identified a relatively small number of climate-resilient areas that, when integrated with existing conservation zones, could help facilitating species' climate adaptation through strategies focused on retention or movement. The size and specific locations of these areas depend on the conservation targets and the climate scenario considered: under the constrained representation target of $T = 100$ km2, the highlighted retention refugia, dispersal chains, plus conservation areas (all SNAC sites) encompass ~23 % of Portugal mainland for both RCPs, which does not add much additional coverage relative to the current conservation areas network. These figures increase to 25 %–26 % with a moderate representation target $T = 500$ km2 and to 31 % when considering the more ambitious conservation target of $T = 1000$ km2 for each species considered (Table 2). Despite these values, the underlying biogeographic patterns consistently highlight the same key regions for conservation expansion, primarily the central-west and the northeast of Portugal (Fig. 9, and Figs. S8, S9, S10, S11).

4. Discussion

Today's conservation challenges are markedly more complex than in the past due to intensified human pressures, leading to increased competition for space and reduced options for conservation. The dynamic spatiotemporal shifts of species' ranges under accelerated climate change refute the notion that merely protecting areas from external human-induced threats will ensure the long-term persistence of species and habitats. This vulnerability has been emphasized by several scientific assessments over the past 20 years (e.g., Hannah et al., 2002; Araújo et al., 2004; Hannah et al., 2005; Araújo et al., 2011; Kujala et al., 2011; de Oliveira et al., 2012; Loyola et al., 2013; Thomas and Gillingham, 2015; Lawler et al., 2020; Coldrey et al., 2022; González-Trujillo et al., 2024). While the connection between biodiversity conservation and

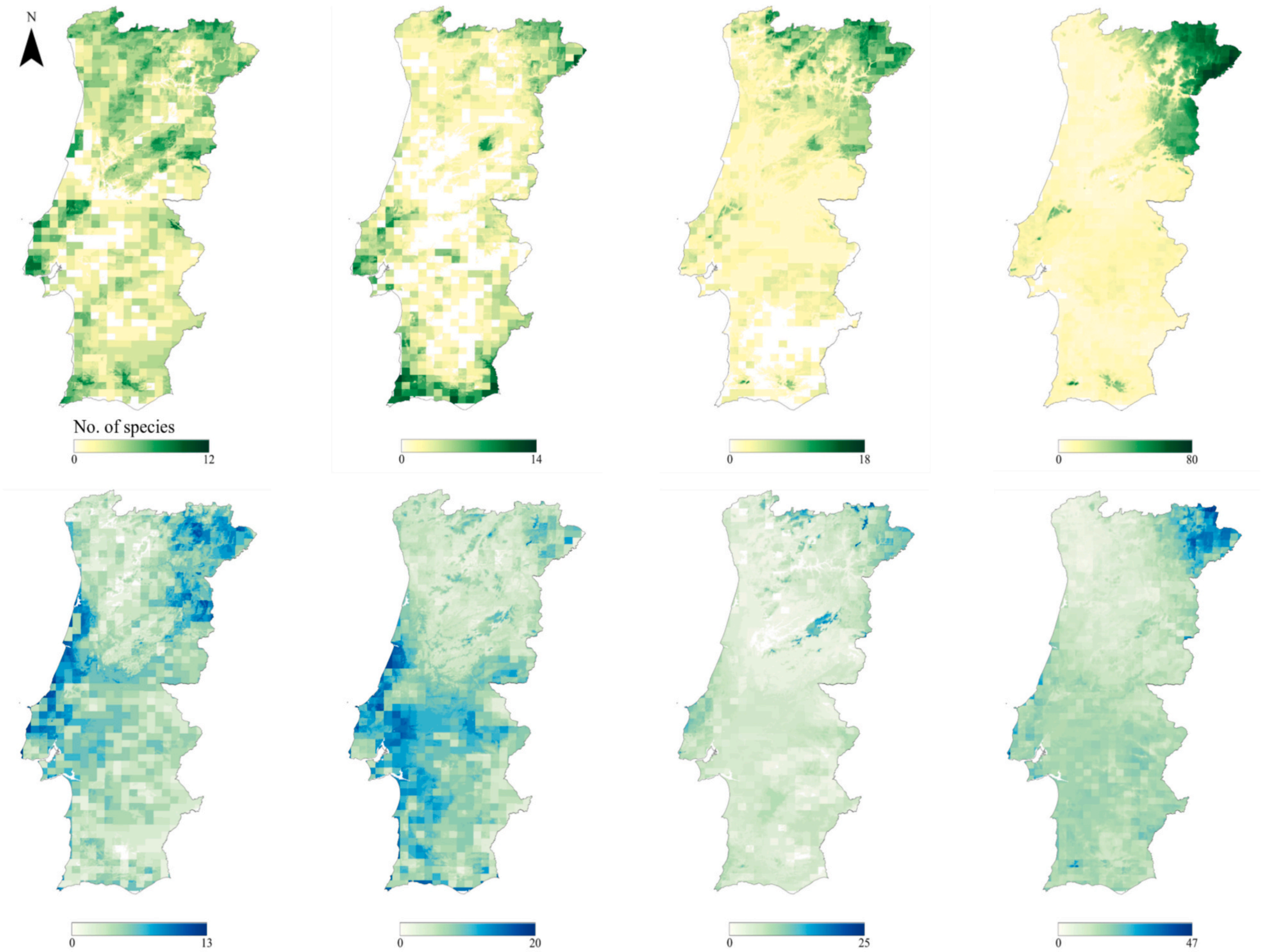


Fig. 5. Richness patterns of vertebrate species displaying climate retention patterns (above) and displacement patterns (below) over the course of the 21st century for: amphibians (1st column); reptiles (2nd column); mammals (3rd column); and birds (4th column). Projections are based on the radiative forcing scenario RCP 6.0. See projections for the RCP 8.5 scenario in Supplementary Fig. S4.

climate change is gradually permeating high-level policy documents (e.g., Araújo, 2009b; Pörtner et al., 2021), substantial progress is still required for it to become mainstream in real-world conservation policy (e.g., Boran and Pettorelli, 2024).

Our study underscores the urgency of this integration by revealing significant projected climate impacts on vertebrate species in Portugal. Birds and mammals are forecasted to face severe range reductions, with median contractions exceeding 78 % under RCP 6.0. Amphibians and reptiles, while somewhat less affected, still face considerable losses, particularly under the more extreme RCP 8.5 scenario. Patterns of retention and displacement refugia highlight the importance of specific regions, notably the central-west ("Oeste") and northeastern ("Trás-os-Montes") areas, as critical for supporting species' climate change adaptation. Moreover, our analysis identifies opportunities to expand Portugal's conservation network by integrating climate-resilient refugia and movement corridors with existing protected areas, consistently highlighting these regions as priorities for facilitating species adaptation to shifting climatic conditions.

By demonstrating how conservation strategies can be connected with spatiotemporal biodiversity dynamics, our findings provide a practical framework for implementing adaptive conservation planning measures. This approach aligns with the goals of the European Biodiversity Strategy for 2030, which emphasizes establishing a coherent network of protected areas covering 30 % of the EU's land and seas, with one-third under strict protection. The strategy further underscores that "*it will be important to set up ecological corridors to prevent genetic isolation, allow for species migration, and maintain and enhance healthy ecosystems*" (EC, 2020). This vision is closely aligned with the objectives of the Global Biodiversity Framework, highlighting the urgency of restoring ecosystems and enhancing biodiversity resilience worldwide (Visconti et al., 2019).

Integrating these principles into mainstream conservation policy is crucial for achieving international conservation targets and safeguarding regional biodiversity in a rapidly changing world. Our study provides a proof of concept for how data-driven, climate-resilient approaches can maximize species persistence, thereby contributing to international efforts to mitigate the impacts of climate change on biodiversity.

4.1. Scientific challenges for guiding protected areas expansion

While much of the progress to be made is regulatory and occurs at the interface of science and policy, the complexity of prioritizing conservation efforts in the face of accelerated spatiotemporal dynamics in biodiversity requires increasingly sophisticated methodologies (Alagador and Cerdeira, 2022). These often involve the integration and analysis of growing volumes of biodiversity data (e.g., Devictor and Bensaude-Vincent, 2016; Anderson et al., 2020), and the development of robust species distribution models that more accurately depict current and future trajectories of species ranges (e.g., Araújo et al., 2019). However, a critical and often overlooked issue is the application of advanced techniques to optimize complementary sets of areas,

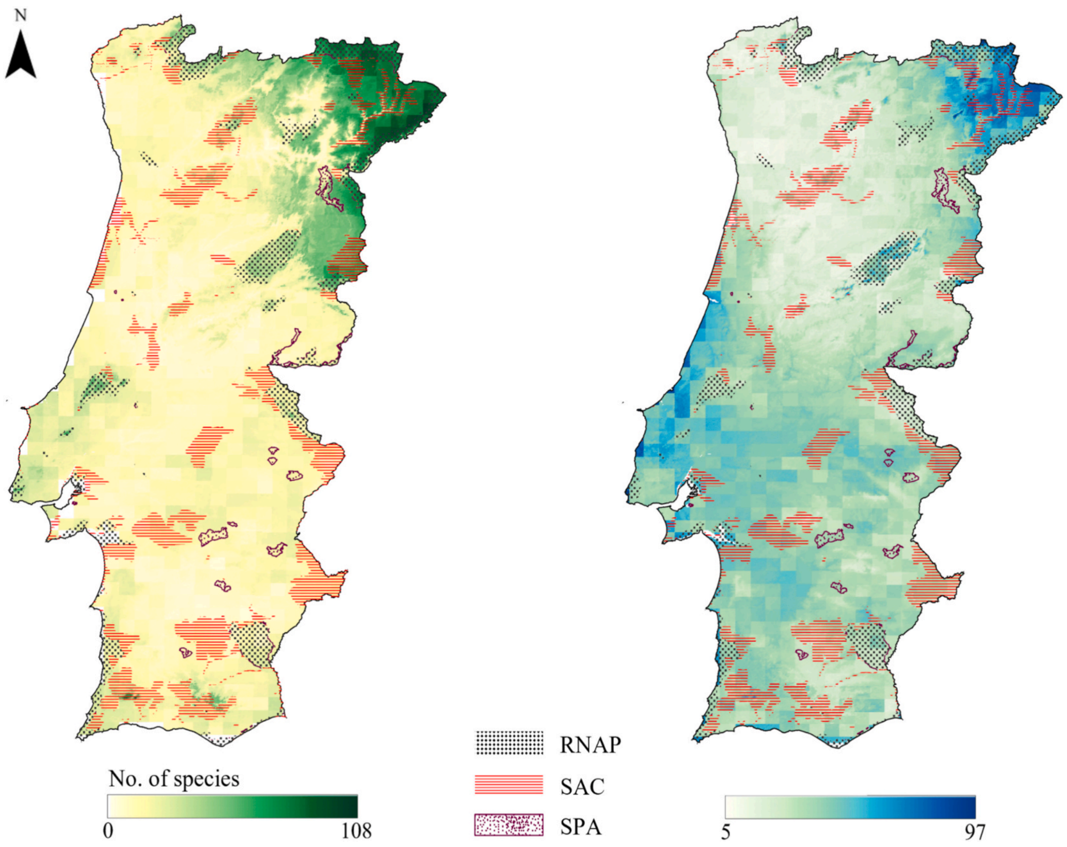


Fig. 6. Species richness of vertebrates showing climate retention patterns (left) and displacement patterns (right), calculated for the course of the 21st century and overlaid on the three types of conservation areas that can be considered within the framework of the European Biodiversity Strategy 2030: RNAP; SAC (Special Areas of Conservation); SPA (Special Protection Areas). Projections are based on the radiative forcing scenario RCP 6.0. See projections for the RCP 8.5 scenario in Supplementary Fig. S5 and analogous results discriminated by taxonomy in Supplementary Figs. S6–7.

Table 1
Average terrestrial vertebrate species richness under retention refugia and displacement conditions in the RNAP (National Network of Protected Areas), SAC (Special Areas of Conservation), SPA (Special Protection Areas), a combination of the three categories (SNAC), and unclassified territory. Areas of SAC and SPA overlapping with RNAP are excluded from the calculation.

	Average species richness			
Conservation areas	Retention refugia		Displacement refugia	
	RCP6.0	RCP8.5	RCP6.0	RCP8.5
RNAP	34	22	28	25
SAC	21	13	27	26
SPA	17	9	25	25
SNAC	26	16	27	25
Non-conserved territory	16	10	26	25

maximizing species persistence across both space and time.

Complementarity-based techniques are particularly important for identifying strategies that maximize the conservation value of protected areas while minimizing the impact of competing demands on the limited land available (Vane-Wright et al., 1991; Pressey et al., 1993). Their application in the context of spatiotemporal conservation prioritization is particularly challenging given that off-the-shelf software have not been developed for this specific purpose. Furthermore, existing spatiotemporal optimization algorithms are based on heuristics, providing only approximations to the optimal solution, and their properties have not yet been fully explored (Phillips et al., 2008; Alagador and Cerdeira, 2017). Moreover, the complexity of prioritizing biodiversity conservation areas can increase depending on the specific formulation of the problem, and current algorithms are still far from considering a realistic range of values and constraints (but see Alagador et al., 2016; Alagador and Cerdeira, 2020). For example, whether one uses continuous measurement of environmental suitability as surrogates for probability of persistence, versus a conversion of these values into estimates of presence-absence, results in different problem formulations. While heuristic algorithms exist to optimize persistence estimates in complementarity-based spatial conservation, using continuous metrics of habitat suitability or probability of persistence (Williams and Araújo, 2000, 2002; Cabeza et al., 2004; Schapaugh and Tyre, 2014), they have not been adapted to handle cases where explicit spatiotemporal structure are accounted for (Alagador et al., 2016). This introduces a range of methodological and ecological uncertainties. First, the conversion of continuous suitability surfaces into presence-absence or presence-only data is highly sensitive to the choice of method (Nenzén and Araújo, 2011), and while an extensive debate exists on how best to make these data transformation no objective guidelines are currently available to standardize this process (e.g., Liu et al., 2005; Jiménez-Valverde and Lobo, 2007; Liu et al., 2013).

Second, while the relationship between occupancy (or suitability) and persistence (or abundance) has been successfully validated in most cases (Araújo et al., 2002; Zuckerberg et al., 2009; Van Couwenberghe et al., 2013; Csergő et al., 2017; Weber et al., 2017; de la Fuente et al., 2021) and disputed in a few others (Sporbert et al., 2020), much of the information contained in suitability data is lost when it is converted into presence and absence. Further complications can arise depending on whether newly selected areas are assumed to fulfil a permanent or temporary role in the conservation network (Alagador et al., 2014), raising the challenge of temporal sequencing and deselection of areas when they lose conservation value (Araújo, 2009b).

In this context, the temporal dynamics of species distributions under

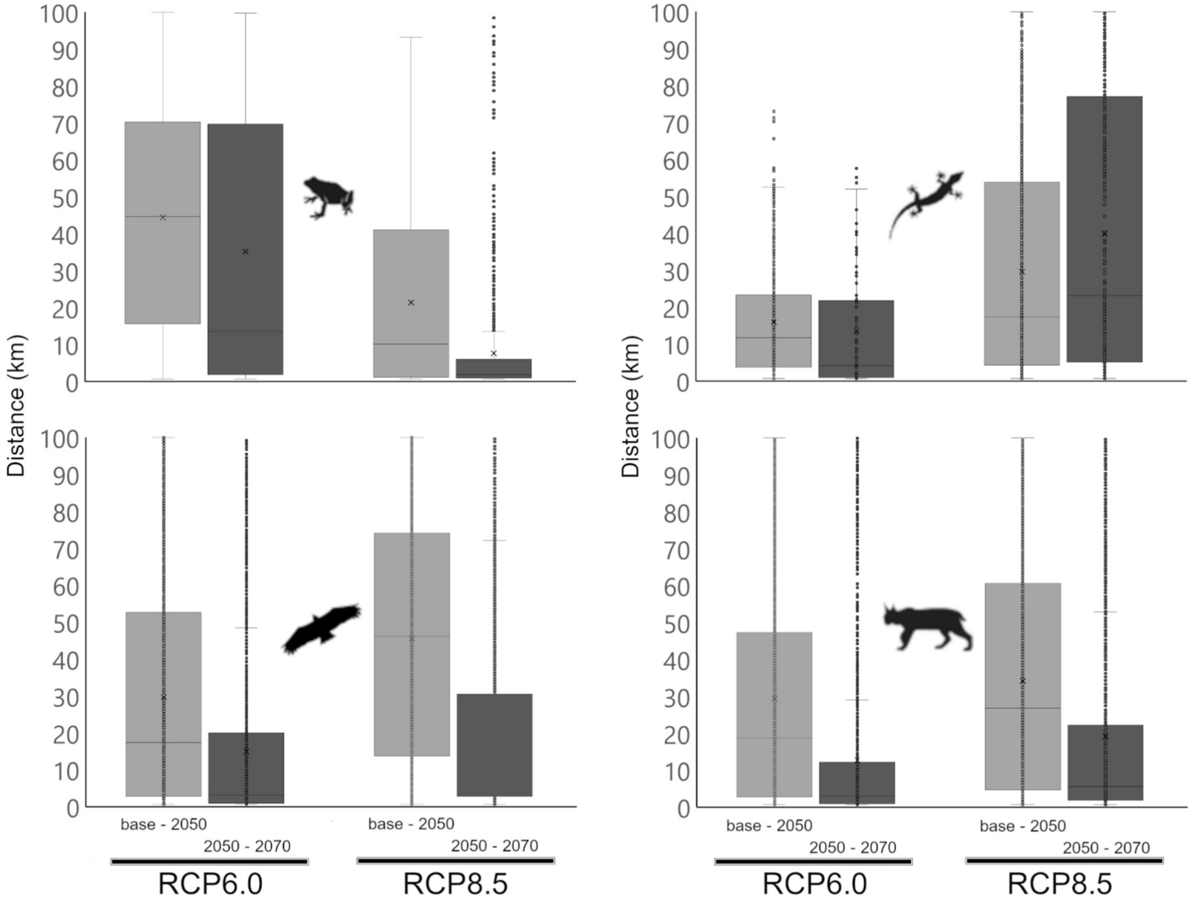


Fig. 7. Dispersal distances required for tracking climate suitability from currently protected areas to refugial areas across taxonomic groups and emissions scenarios. Values correspond to the two-time intervals assessed (current period–2050 and 2050–2070) for RCP 6.0 and RCP 8.5. Amphibians: upper left; reptiles: upper right; birds: lower left; mammals: lower right. Boxes represent the 2nd and 3rd quartiles, vertical lines indicate median values, crosses represent mean values, whiskers define the interquartile range, and points are outliers.

climate change could be better captured by incorporating multiple decadal time steps rather than relying on only three snapshots, as done in the current study. Dynamic approaches—whether through explicit modeling or interpolated transitions—would allow for finer assessments of persistence and turnover. These could also facilitate the integration of interactions between climate and land-use change as well as the inclusion of non-climatic constraints such as habitat availability and biotic interactions(e.g., Fordham et al., 2013). In parallel, connectivity modeling could be enhanced by accounting not only for climate-informed structural features—such as topography, slope orientation, and moisture availability—but also for landscape permeability. Human disturbance, including urbanization, agricultural development, and infrastructure, can significantly reduce connectivity by impeding species movement across the landscape. Incorporating such factors through resistance surfaces or cost-distance metrics would refine corridor identification, particularly in more fragmented regions. Additionally, species-specific variation in dispersal capacity could be better represented by adopting differentiated dispersal scenarios based on functional traits (e.g., body size, dispersal mode). Together, these extensions would improve the ecological realism and predictive robustness of connectivity assessments under climate change.

Relatedly, another important direction for improving realism lies in the consideration of climate variability and extremes. Beyond long-term climatic means, the inclusion of metrics for climatic seasonality (Tonkin et al., 2017) and the frequency and intensity of extreme weather events—known to be critical drivers of biodiversity change (González-Trujillo et al., 2023) and protected areas vulnerability (González-Trujillo et al., 2024)—could greatly enhance the robustness of distribution forecasts. While integrating all of these ecological, climatic, and land-use factors into a single modeling framework remains computationally and methodologically demanding, doing so would increase the credibility and interpretability of long-term conservation planning.

Additionally, spatial conservation planning protocols could evolve to incorporate more diverse objective functions, extending beyond species representation. For example, future planning frameworks might aim to maximize rewilding potential (e.g., Araújo and Alagador, 2024), account for recreation value (e.g., Lavorel et al., 2020), or integrate multiple cultural and societal values (e.g., Tiago et al., 2017), thereby broadening the relevance and acceptance of conservation policies (Araújo, 2025).

Finally, while we did not perform parameter tuning in our species distribution modeling framework, we adopted an alternative strategy in which underperforming models are either discarded or downweighted within the ensemble consensus. This approach, widely used in ensemble modeling (Araújo and New, 2007; Garcia et al., 2012; Rose et al., 2024), strikes a balance between computational efficiency and predictive reliability—particularly valuable in large-scale, multi-species applications. Although parameter tuning can improve individual model performance (Elith and Graham, 2009; Hao et al., 2020), our ensemble-based strategy provides a pragmatic and scalable solution for the aims of this study.

4.2. *Practical challenges for guiding protected areas expansion*

Clearly, spatial conservation prioritization can advance in both the sophistication of the methodologies used and the realism of the

Fig. 8. Direction and magnitude of biodiversity flows (vertebrate displacement chains originating in the SNAC) in response to climate change (RCP 6.0). Flows are calculated based on a climate safety target of 500 km^2 for each species.

Table 2
Proposed conservation areas coverage resulting from applying three conservation targets and two greenhouse gas emissions scenarios towards 2070. Total Area (Km^2): Area covered by climate refugia and SNAC; Relative area (%): percentage of Portugal's mainland covered by climate refugia and SNAC.

	Conservation targets					
	100 Km^2		500 Km^2		1000 Km^2	
	Total area (Km^2)	Relative area (%)	Total area (Km^2)	Relative area (%)	Total area (Km^2)	Relative area (%)
RCP 6.0	20,193	23	22,504	25	27,643	31
RCP 8.5	20,145	23	23,201	26	27,576	31

underlying assumptions. For example, an often-neglected issue is how the resolution of data affects conservation priorities, whether in the traditional context of static conservation prioritization (e.g., Araújo et al., 2005b) or in the less common dynamic processes that account for climate change (e.g., Dupont-Doaré and Alagador, 2021). This highlights that, regardless of the robustness of the spatial prioritization protocol, data will always be a limiting factor. However, an even greater limitation is the willingness of decision-makers to allow the scientific process to guide the selection of locations and the allocation of resources for biodiversity conservation. If scientific solutions for prioritization were in higher demand, more resources would be allocated to this area, generating new critical data for decision-making, and greater numbers of researchers would be devoted to developing more advanced methods and tools.

The unfortunate reality is that, despite the science of systematic conservation planning being nearly 40 years old (Kirkpatrick, 1983), in many European countries, data-driven, quantitative, approaches remain more theoretical than practical, with policy decisions being largely driven by expert judgment or political expediency. Portugal is no exception. Historically, protected area prioritization has largely been established through a bottom-up approach, responding to opportunities and pressures as they arose (e.g., Queirós, 2012). In contrast, the Europe-wide Natura 2000 network was created through a top-down process, guided by European legislation and administered by the European Commission. Following the commitments of EU member states to meet the goals of the European Biodiversity Strategy 2030, which include expanding protected areas to cover 30 % of land and sea, there was brief interest from governmental bodies in using spatial conservation methodologies to guide the selection of these areas (Araújo et al., 2022). However, just months before its downfall, the XXIII government of the Portugal's 3rd Republic chose to overlook existing scientific recommendations. Instead, they took a controversial step through the Council of Ministers to ostensively meet the 30 % conservation coverage target by 2030 by administratively reclassifying areas with lose conservation status, such as RAMSAR Sites, UNESCO Geoparks, and Biosphere Reserves, as fully protected (Fig. 10). Combined with existing conservation areas (SNAC sites), the reclassified territory would amount to approximately 34 % of the country, thus exceeding the European and international target of 30 %.

While RAMSAR sites generally coincide with nationally designated protected areas and Natura 2000 sites, adding little to existing conservation areas, Geoparks and Biosphere Reserves often encompass vast areas beyond the existing conservation areas included in the SNAC (National System of Classified Areas). These areas frequently include motorways, cities, industries, and other regions with limited biodiversity value. The decision to meet—or even exceed—the 30 % conservation target by administratively reclassifying areas originally designated for purposes other than biodiversity conservation effectively sidesteps established scientific knowledge and critical consultative processes essential for informed decision-making in conservation planning (e.g., Díez et al., 2015; Huber et al., 2023).

At the time of writing, it is unclear what direction the new governments will pursue. Nevertheless, the prior government's approach of favoring expediency over thorough scientifically grounded conservation strategies sends a concerning message with potentially dire implications. By attempting to meet the 30 % EU biodiversity target for 2030 through administrative reclassification of areas with lose connection with the European and international biodiversity targets, the government failed to strategically select the additional 7 % required to complement existing conservation areas. This approach, if finally adopted, would incur significant costs in two key areas.

Firstly, this approach ignores existing knowledge on the impacts of climate change on biodiversity, leading to the neglect of crucial climate change refugia vital for long-term conservation. The proposed reclassification of areas ignores the western refugia, north of Lisbon, which our analysis identifies, along with the 'Trás-os-Montes' region in the

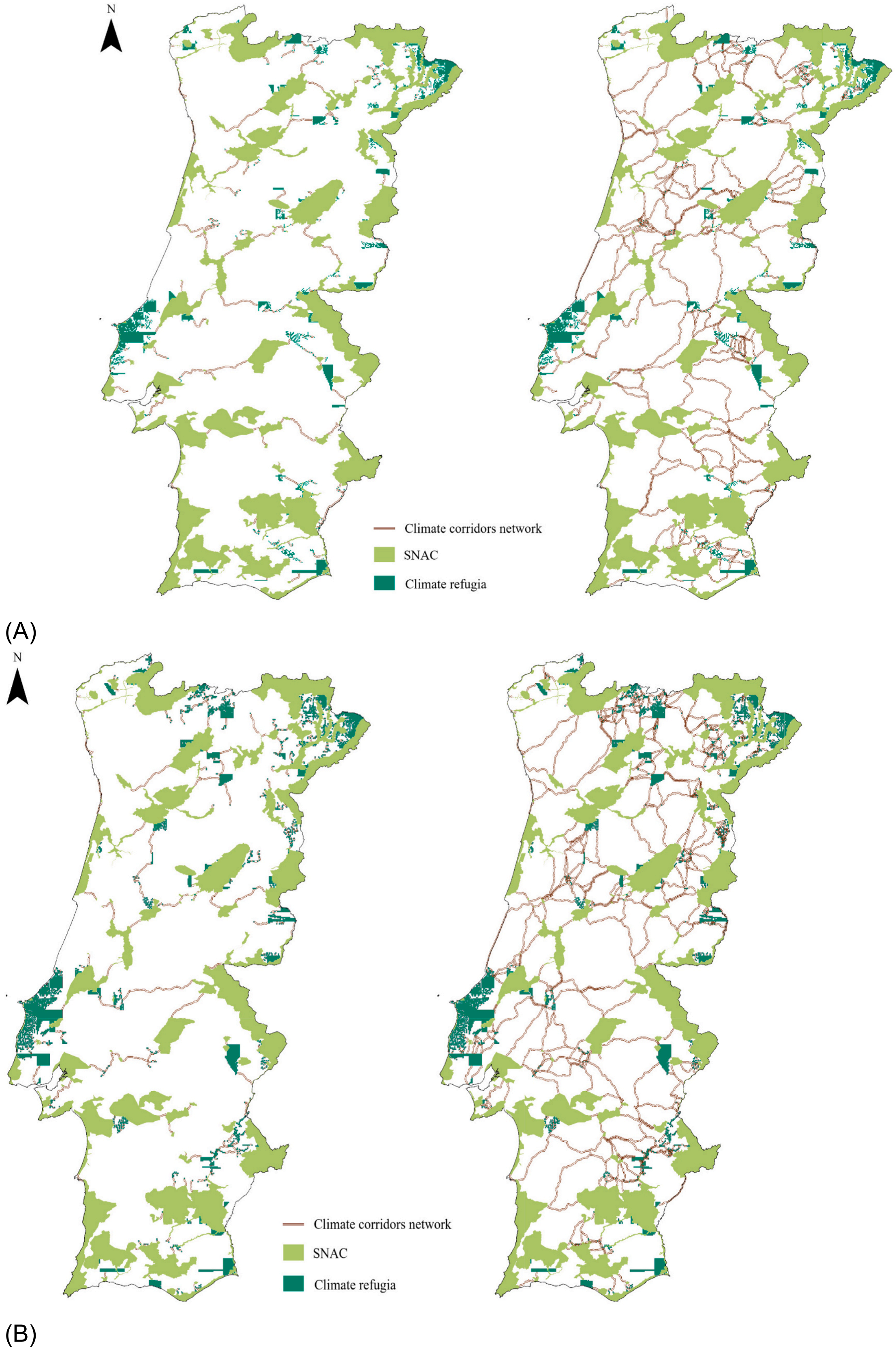


Fig. 9. Alternative proposals for the Biodiversity Climate Adaptation Framework (BCAF) targeting 500 km2 of climate safety per species in the RCP 6.0 scenario (A) and RCP 8.5 (B): globally optimized structural connectivity scenario (left) and regionally optimized scenario (right). The combined areas of RNAP (National Network of Protected Areas), SAC (Special Areas of Conservation), and SPA (Special Protection Areas) are included, as well as the optimized network of climate refugia (retention and dispersal chains). See proposals targeting 100 km2 and 1000 km2 in Supplementary Figs. S7–7, and analogous results for the RCP 8.5 scenario in Supplementary Figs. S9–11.

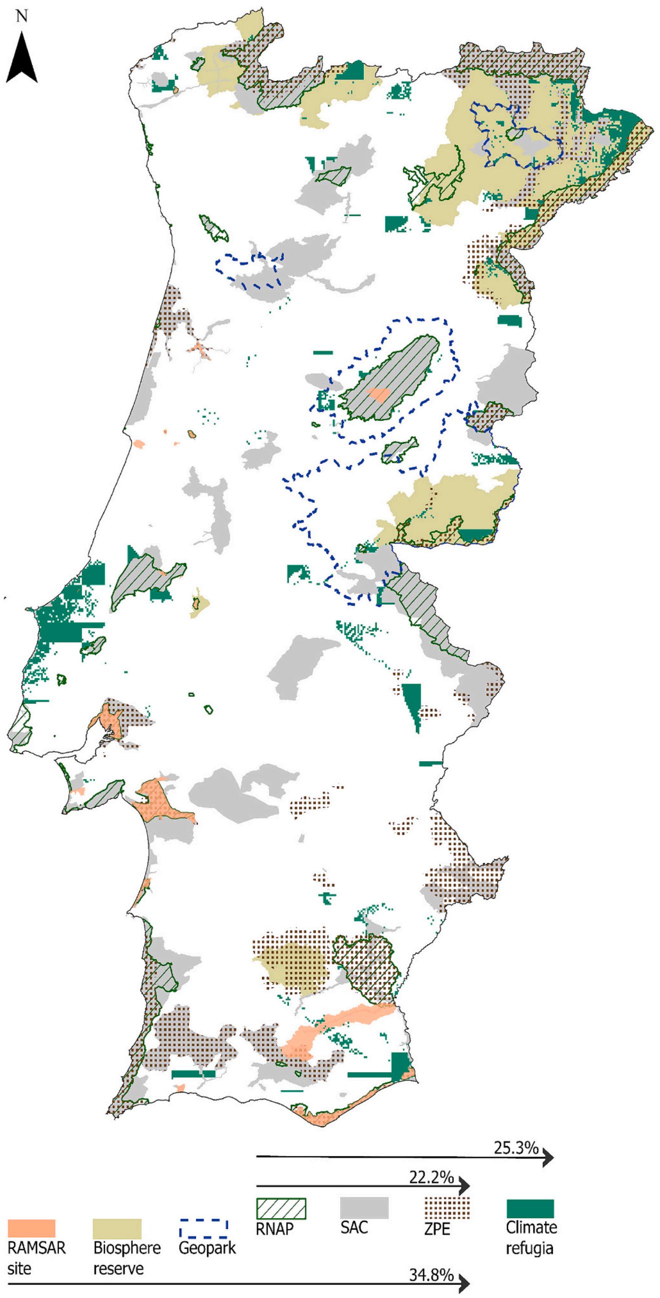


Fig. 10. Overlay of the different types of conservation areas in Portugal. It includes the RAMSAR sites, Geoparks, and Biosphere reserves that currently are not included as part of the SNAC ("Sistema Nacional de Áreas Classificadas", or National system of Classified Areas) and the proposed climate resilient conservation area network depicted in Fig. 8A.

northeast, as the most important climate refuges in Portugal. The western refugia is projected to play a critical role in protecting the biodiversity currently supported by adjacent protected areas (Fig. 9). This oversight could severely compromise the effectiveness of conservation efforts in regions that are key to the resilience of biodiversity in the face of changing climate conditions.

Secondly, by designating extensive areas of low biodiversity relevance as protected, the decision would likely dilute the effectiveness of conservation efforts, spreading resources too thinly and reducing focus on areas that truly need protection based on scientific assessments. Notably, we found that achieving a 31 % conservation coverage—less than the 34 % proposed by the government—would still meet the most ambitious conservation target considered in our study, ensuring the protection of approximately 1000 km^2 of habitat per species over the 21st century, regardless of the climate change scenario considered. With a less ambitious target of protecting 500 km^2 of habitat per species, the required conservation coverage could drop to 25–26 %, depending on the intensity of climate change. Thus, the government's proposed solution would not only lock in a greater area for conservation—incurring inevitable opportunity costs—but also fail to meet the objectives it has committed to under European law, which mandate expanding conservation areas in a way that reflects the challenges climate change poses to biodiversity. Such weak alignment of conservation areas designation with policy targets and operational objectives involves risks that are well documented: "targets and objectives can be achieved while making little difference to the conservation of biodiversity" (Pressey et al., 2015).

Moreover, the approach reflects outdated conservation methodologies that were already scrutinized and criticized in the late-20th century (Pressey and Nicholls, 1989; Pressey et al., 1993). In today's context, where biodiversity challenges are vastly more complex and interconnected their conservation ineffectiveness and cost inefficiency is to be expected (Hannah et al., 2007). By not adhering to 21st-century best practices, which emphasize data-driven and stakeholder-supported decisions, political and administrative expediency as a strategy for prioritization of conservation areas compromises both the ecological integrity of the regions and the credibility of the initiatives (Maxwell et al., 2020). It is crucial for conservation policies addressing the 2030 commitments to align with modern conservation science, ensuring that strategies are both ecologically effective and socially supported, to truly meet the agreed biodiversity targets.

5. Conclusions

The challenges facing biodiversity conservation today are far more complex than in the past due to intensified human pressures and the dynamic effects of climate change. Traditional approaches, which often rely on protecting static areas from external threats, are no longer sufficient for ensuring species persistence in the long term. Scientific assessments over the past two decades have highlighted the need for conservation strategies that account for the spatiotemporal dynamics of species distributions under climate change. While progress has been made in integrating biodiversity conservation with climate change adaptation in high-level policy discussions, significant gaps remain in the practical implementation of data-driven, quantitative approaches to conservation planning.

Methodologically, spatial conservation prioritization has advanced with the development of sophisticated tools such as species distribution models and complementarity-based techniques. However, these tools are rarely used, partly because off-the-shelf software that fully integrates models of spatiotemporal biodiversity dynamics with optimization tools is still lacking. Additionally, existing heuristic near-optimal algorithms have not been comprehensively tested, and fully optimal approaches struggle to handle data and problems of such complexity. The challenge of using incomplete species coverage of the tree of life also poses significant limitations, as conservation planning often relies on a subset of taxa with sufficient data. For example, in this study, we were unable to include plants and invertebrates due to data constraints, potentially overlooking important areas critical for biodiversity conservation. Other unresolved issues, such as the consequences of using data at insufficiently fine resolution, challenges in suitability-persistence relationships, and the conversion of continuous data into presence-absence formats, further complicate the use of quantitative tools for conservation planning.

The case of Portugal serves as an example of the practical challenges associated with implementing effective conservation strategies. While some European initiatives like the Natura 2000 network have been developed through top-down processes, Portugal has largely relied on bottom-up, opportunistic conservation efforts. Recent actions to reclassify areas with limited biodiversity value in order to meet the

European Biodiversity Strategy 2030 goals highlight the risks of prioritizing expediency over scientifically grounded conservation efforts. This approach not only undermines long-term conservation effectiveness but also disregards the importance of climate change refugia and other critical habitats for biodiversity resilience.

The spatial conservation planning protocol developed here is not limited to Portugal and could also be applied to benefit other regions. Sophisticated prioritization methods like those developed in this study are more easily implemented in data-rich regions such as Europe, Australia, China, Japan, North America, and South Africa. However, the greatest need and opportunities lie in tropical regions. These areas, with their high levels of restricted-range endemism, serve as global biodiversity hotspots and are under immense pressure from habitat loss and climate change. As such, they represent high-priority targets for conservation efforts that integrate spatiotemporal biodiversity dynamics. Ultimately, achieving the ambitious goals of the 2030 biodiversity strategy will require decision-makers to embrace scientifically robust, data-driven methodologies for conservation prioritization. By aligning conservation efforts with modern ecological science, nations can ensure that protected areas are strategically selected to maximize species persistence and address the growing threats posed by climate change.

CRediT authorship contribution statement

Miguel B. Araújo: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Diogo Alagador:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis. **Babak Naimi:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis. **Dora Neto:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation. **Alejandro Rozenfeld:** Software, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111249.

Data availability

Data will be made available on request.

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