

CONTRIBUTED PAPERS

Effective conservation planning of Iberian amphibians based on a regionalization of climate-driven range shifts

Diogo Alagador^{1,2} 

¹The Biodiversity Chair, Institute for Advanced Studies and Research, Universidade de Évora, Évora, Portugal

²MED - Mediterranean Institute for Agriculture, Environment and Development, CHANGE - Global Change and Sustainability Institute, Universidade de Évora, Évora, Portugal

Correspondence

Diogo Alagador, Institute for Advanced Studies and Research, Universidade de Évora, Évora, Portugal
Email: alagador@uevora.pt

Article Impact Statement: Effective conservation plans depend on assessments of when areas will be functional for species to adapt to climate change.

Funding information

Fundação para a Ciência e a Tecnologia, Grant/Award Number: UIDB/05183/2020

Abstract

Amphibians are severely affected by climate change, particularly in regions where droughts prevail and water availability is scarce. The extirpation of amphibians triggers cascading effects that disrupt the trophic structure of food webs and ecosystems. Dedicated assessments of the spatial adaptive potential of amphibian species under climate change are, therefore, essential to provide guidelines for their effective conservation. I used predictions about the location of suitable climates for 27 amphibian species in the Iberian Peninsula from a baseline period to 2080 to typify shifting species' ranges. The time at which these range types are expected to be functionally important for the adaptation of a species was used to identify full or partial refugia; areas most likely to be the home of populations moving into new climatically suitable grounds; areas most likely to receive populations after climate adaptive dispersal; and climatically unsuitable areas near suitable areas. I implemented an area prioritization protocol for each species to obtain a cohesive set of areas that would provide maximum adaptability and where management interventions should be prioritized. A connectivity assessment pinpointed where facilitative strategies would be most effective. Each of the 27 species had distinct spatial requirements but, common to all species, a bottleneck effect was predicted by 2050 because source areas for subsequent dispersal were small in extent. Three species emerged as difficult to maintain up to 2080. The Iberian northwest was predicted to capture adaptive range for most species. My study offers analytical guidelines for managers and decision makers to undertake systematic assessments on where and when to intervene to maximize the persistence of amphibian species and the functionality of the ecosystems that depend on them.

KEYWORDS

adaptation, climate change, connectivity, conservation plan, cost-effectiveness, decision support, optimization, refugia

Planeación efectiva de la conservación de anfibios ibéricos con base en una regionalización del rango de cambios causados por el clima

Resumen: El cambio climático afecta severamente a los anfibios, en particular en las regiones en donde prevalecen las sequías y el agua es escasa. La extirpación de los anfibios dispara efectos en cascada que interrumpen la estructura trófica de las redes alimenticias y los ecosistemas. Por lo tanto, son esenciales los análisis especializados en el potencial de adaptación espacial de las especies anfibias ante el cambio climático para proporcionar las directrices para su conservación efectiva. Usé predicciones de la ubicación de climas adecuados para 27 especies anfibias en la Península Ibérica a partir de un periodo base hasta 2080 para tipificar los rangos de las especies cambiantes. Usé el tiempo en el cual se

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial License](https://creativecommons.org/licenses/by-nc/4.0/), which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Conservation Biology* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

espera que estos tipos de rango sean funcionalmente importantes para la adaptación de una especie para identificar refugios completos o parciales; las áreas con mayor probabilidad de ser el hogar de las poblaciones que se mudan hacia nuevos terrenos con climas más adecuados; las áreas con mayor probabilidad de recibir poblaciones después de la dispersión adaptativa por el clima; y áreas con clima inadecuado cerca de las áreas adecuadas. Implementé un protocolo de priorización de área para cada especie y así obtener un conjunto completo de áreas que proporcionarían la máxima adaptabilidad y en donde las intervenciones de manejo deberían priorizarse. Un análisis de conectividad identificó en dónde serían más efectivas las estrategias facilitadoras. Cada una de las 27 especies tuvo requerimientos espaciales distintos, pero, común a todas las especies, se pronosticó un efecto de cuello de botella para el 2050 debido a que las áreas de origen para la dispersión subsecuente tenían una extensión pequeña. Tres especies emergieron como complicadas de mantener hasta el 2080. Mi estudio ofrece directrices analíticas para que los gestores y los órganos de decisión realicen evaluaciones sistemáticas de en dónde y cuándo intervenir para maximizar la persistencia de las especies anfibias y la funcionalidad de los ecosistemas que dependen de ellas.

PALABRAS CLAVE

adaptación, cambio climático, conectividad, optimización, plan de conservación, refugios, respaldo a la decisión, rentabilidad

【摘要】

两栖动物受到气候变化的严重影响,特别是在干旱和水资源匮乏的地区。两栖动物的灭绝会引发级联效应,破坏食物网和生态系统的营养结构。因此,对两栖动物在气候变化下的空间适应潜力评估对指导其有效保护至关重要。研究者基于对伊比利亚半岛27种两栖动物从基线期到2080年的适宜气候区预测,划分了物种范围变化的类型。利用这些范围类型对物种适应具有重要功能的预期时间,研究者确定了全部或部分的避难所、最有可能为迁入新的气候适宜区的种群提供栖息地的地区、最有可能在气候适应性扩散后容纳种群的地区,以及气候适宜区附近气候不适宜的地区。研究者还为每个物种制定了确定优先保护区域的方法,以确定能提供最大适应性且应优先考虑管理干预措施的地区。此外,研究者通过连接度评估得到了对促进性策略最有效的区域。这27个物种各自有不同的空间需求,但它们都有一个共同点,即由于后续扩散的源区范围很小,它们预测到2050年都会面临瓶颈效应。有三个物种可能难以续存至2080年。伊比利亚西北部被预测覆盖了大多数物种的适应性分布范围。本研究为管理者和决策者提供了分析指南,可以帮助其系统地评估应在何时何地进行干预,以最大限度地维持两栖动物续存,并维持依赖它们的生态系统功能。【翻译:胡怡思;审校:聂永刚】

合作类型: 适应, 气候变化, 连接度, 保护计划, 成本效益, 决策支持, 优化, 避难所

INTRODUCTION

Amphibians fulfill critical roles in the maintenance of ecological processes (Hocking & Babbitt, 2014), being key elements in the balance of energy and nutrients between freshwater and terrestrial realms (Earl et al., 2022; Fritz & Whiles, 2018). They also control insect-borne diseases and seed dispersal; affect nutrient cycles and primary productivity in ponds. Fossorial species alter the physical properties of soils (e.g., water infiltration, oxygen, and carbon uptake). In ephemeral ponds of temperate and Mediterranean regions, amphibians fill the trophic role of ichthyofauna (Clancy, 2017). Their great sensitivity to environmental changes and a high degree of specialization make them effective ecological indicators (Stapanian et al., 2015). Their sensitivity is evidenced by abrupt population fluctuations. These

fluctuations signal the need for urgent habitat restoration, which indirectly favors populations of other less responsive taxa (Qazi & Ashok, 2012). Loss of amphibians may trigger detrimental cascading effects leading to large disturbances of ecosystems.

Amphibians are particularly susceptible to climate change because they have relatively small ranges and are greatly dependent on the quality of habitats through which they disperse (de Vries et al., 2017). At local scales, amphibian demographic rates (Ficetola, 2015) are affected directly by temperature and water availability (Taylor et al., 2013). Typically, for some species, local biophysical conditions, unrelated to weather, militate against climate fluctuations by providing microrefugia (Ashcroft et al., 2012). However, the current magnitude and rate of regional climate change is negating the balancing effect of these local biophysical factors, leading to negative changes in metapopulation

dynamics (Suggitt et al., 2018). The loss of microrefugia is of particular concern for species with limited dispersal. To conserve amphibians, actions must be scaled up from the provision of local refugia to the conservation or restoration of larger areas with transient ecological value, where climate-driven adaptive movements are likely to occur (Alagador et al., 2014). Assisted colonization plans may be the last resort for saving highly threatened species.

Effective conservation depends on careful planning, ideally, with a low impact on conventional socioeconomic activities. Understanding of species' responses to climate change at temporal and spatial scales and evaluation of shifts in the extent and proximity of climatically suitable areas over time are needed to provide guidelines for the effective protection of species and their adaptive habitats (Alagador et al., 2016).

The Iberian Peninsula is home to 27 species of amphibians that are phylogeographically distinct from central European herpetofauna (Dufresnes & Perrin, 2015; Gómez & Lunt, 2007; Loureiro et al., 2008; Pleguezuelos et al., 2002). Of these 27 species, 10 are endemic to the Iberian Peninsula, five also occur in restricted regions in southern Europe, and 12 are distributed throughout Europe. Because the Iberian Peninsula is expected to undergo extensive periods of dryness, at short to medium terms (Cardoso Pereira et al., 2020), to be exposed to extreme temperatures (Viceto et al., 2019), and to be invaded by species from North Africa (Ascensão et al., 2021), the persistence of Iberian amphibians is a matter of extreme concern.

Several studies have been carried on the Iberian Peninsula to predict the responses of amphibians to plausible climate change scenarios (Carvalho et al., 2011; Carvalho et al., 2019; Enriquez-Urzelai et al., 2019; Rodríguez-Rodríguez et al., 2020a; Sillero, 2021). None, however, provide a framework for strategic allocation of conservation actions in space and time in a manner that maximizes the persistence of amphibians over the long term (i.e., 50 years). I aimed to close this gap and deliver the first comprehensive assessment of the potential spatial adaptive responses of amphibians to climate change in the Iberian Peninsula. The analysis aims to support the design of appropriate climate-change adaptation strategies through time. I predicted species' potential distributions from a baseline period to 2080 based on species-specific dispersal windows that outlined potential adaptive rearrangements of species' ranges. The time at which each area is expected to be functionally important for the adaptation of a species was used to classify areas into range types: full or partial refugia (i.e., areas with extensive periods of climatic suitability); leading or source areas for dispersal (i.e., areas most likely to be home to populations moving into new climatically suitable grounds); colonizing areas (i.e., areas most likely to receive populations after climate adaptive dispersal); and gap areas (climatically unsuitable areas near suitable areas and where assisted colonization may provide good prospects for species' persistence). A cohesive set of areas adequately representing each species' range type with the maximum functionality was obtained through a spatial prioritization model. Finally, I assessed landscape connectivity for each species using circuit theory complemented by a graph-based

minimum spanning tree connectivity to highlight the areas that best favor the spatial adaptive responses of each species in prioritized areas.

METHODS

I used the amphibian taxonomy in the amphibian atlases of Portugal (Loureiro et al., 2008) and Spain (Pleguezuelos et al., 2002) to obtain presence and absence records of 27 amphibian species in a 10×10 km grid covering the Iberian Peninsula (Appendix S1). For comparative purposes, a more recent taxonomy of amphibian species is available (Speybroeck et al., 2020).

Ensembles of bioclimatic niche models were used to predict the spatial and temporal distribution of suitable climates for each species. Climate data (average annual minimum temperature, average annual maximum temperature, and average annual total precipitation) were gathered from WordClim 2.1 (Fick & Hijmans, 2017). This parsimonious set of variables covers important climatic axes that limit the distribution of terrestrial coldblooded species and avoids model overfitting: thermal amplitude, which reflects activity time (maximum and minimum temperatures); the minimum amount of energy available for the activity of species (minimum temperature); and water availability (annual precipitation). To make bioclimatic analyses straightforward, the three variables were considered equally relevant for the 27 species assessed. Data for those variables refer to three periods: 1970–2000 (baseline period, which for convenience I assumed to be stable until 2020), 2041–2060 (referred to as 2050), and 2061–2080 (referred to as 2080). I used these periods so there would be similar 30-year time intervals among the periods assessed. Grid cell resolution was 5×5 arcmin grid (approximately 100 km²) for calibration data and 30×30 arcsec (approximately 1 km²) for projection data.

Future climate data were derived from a set of selected global circulation models (GCMs) that incorporate the most pressing shared socioeconomic pathway scenario (SSP585). The 10 GCMs were built under the Coupled Model Intercomparison Project Phase 6 and were selected to represent the highest variability in predictions of the thermic and water-based climatic components: BCC-CSM2-MR, CMCC-ESM2, GISS-E2-1H, HadGEM3-GC31-LL, INM-CM5-0, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0, and UKESM1-0-LL (complete description of GCMs at <https://pcmdi.llnl.gov/CMIP6/>).

Bioclimatic models were run in the sdm package (Naimi & Araújo, 2016) in R (R Development Core Team, 2021) with 11 model typologies (generalized linear models, generalized additive models, classification and regression trees, boosted regression trees, random forests, multiple discriminant analysis, supported vector machines, multivariate adaptive regression splines, maximum entropy, bioclimatic envelope, and domain) and default settings. For each species, 1000 pseudoabsence points were randomly recorded as background data. A k -fold cross-validation ($k = 5$) was established, within which occurrence data were randomly partitioned into five sets. Each set was used to calibrate each model while leaving the remaining

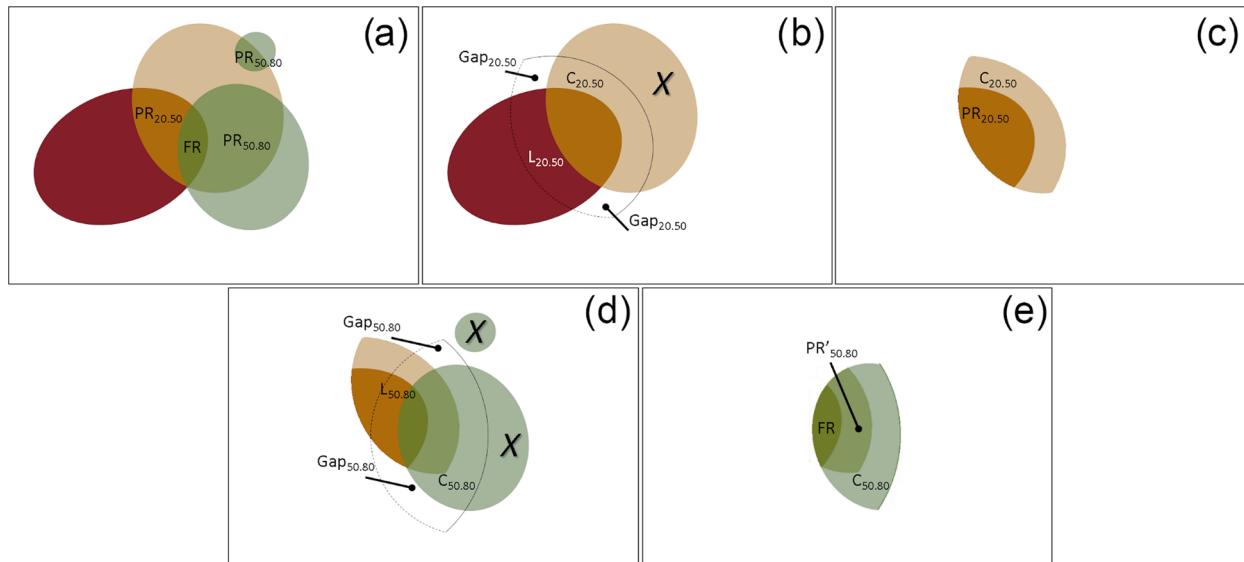


FIGURE 1 The analytic framework defining the typologies of adaptive range shifts of amphibian species over time (shapes, climatic suitability regions; dark red, 2020; beige, 2050; green, 2080): (a) transient partial refugia from 2020 to 2050 ($PR_{20,50}$) and from 2050 to 2080 ($PR_{20,50}$) and full stable refugia (FR); (b) leading range areas in 2020 ($L_{20,50}$), colonizing ranges from 2020 to 2050 ($C_{20,50}$), and gap areas ($Gap_{20,50}$) (solid line, areas within the maximum dispersal range from 2020 to 2050 such that in 2050 over this range the climatically suitability regions will not be colonized [cross]; dashed line, range of areas in 2020 [leading range areas] serving as sources for colonization in 2050); (c) climatic suitability area likely to be colonized in 2050 (encompasses partial refugia and colonizing areas in 2050); (d) leading ranges in 2050 ($L_{50,80}$), colonizing areas in 2080 ($C_{50,80}$), and gap areas ($Gap_{50,80}$) (graphic elements as in [b]); and (e) climatically suitable area likely to be colonized in 2080 (encompasses full refugia, colonizing section of the partial refugia, and the colonizing areas from 2050)

four sets for validation. In each calibration stage, 20% of randomly selected background points were used alongside 20% of occurrence data. Fifty-five models (5×11) were produced for each species, and their performance was evaluated based on area under the curve (AUC) scores. Models were projected at 1-km² grid cell resolution for 2020, 2050, and 2080 periods. Individual models were combined via an ensemble approach (Araújo & New, 2007) using an AUC-weighted average. Squared AUC scores served as weights to give higher scores to the better-performing models. Finally, 0–1 suitability scores were converted to binary data by calculating the suitability score that minimized the difference between sensitivity (true positive rate) and specificity (true negative rate) (Appendix S1).

For each species, potential occurrence areas in the years 2020, 2050, and 2080 were partitioned into areas that delineated a sequence of potential climate-adaptive regions (Figure 1). Full refugia depict the areas occupied in 2020 (the baseline period) that remain climatically suitable in 2050 and 2080. Partial refugia encompass the areas potentially suitable in two consecutive periods of time (2020–2050 and 2050–2080). Herein, partial refugia are not constrained by dispersal processes and may emerge in regions far from occupied areas in 2020.

The remaining adaptive range areas were defined sequentially based on species' dispersal capabilities (Table 1). Potential leading areas for adaptive displacement (i.e., sourcing grounds) corresponded to 30 km (assuming a 1 km displacement per year) around climatically suitable regions in period $t+1$ that overlapped with occurrence (or potentially occurrence) areas in the previous period (t). In the opposite direction, potential areas for colonization in $t+1$ corresponded to regions

that overlapped the 30 km surrounding occurrence areas (or potential occurrence areas) in t coinciding with climatically suitable regions in $t+1$. Areas with no suitable climates but that would be reachable by species from occurrence areas in t and from potentially suitable areas in $t+1$ were gap regions (Appendix S4). Dispersal rates are very idiosyncratic and highly dependent on species' requirements, life-history traits, and the environmental context. A dispersal rate of 1 km/year assumes abnormal, extreme individual dispersers, which may drive the spatial adjustments of amphibian species (Pittman et al., 2014).

For each species, an optimized area selection approach was implemented to highlight the areas needing priority conservation focus at the minimum cost (i.e., adaptive resistance). I used the R package *prioritizr* (Hanson et al., 2022) and assumed that cost to protect each 1-km² grid cell (a resistance score) is closely related to local characteristics linked to climate buffering capacity and to levels of predictive uncertainty affecting suitability predictions. Whenever feasible, a representation target for each range type was set to 1000 km², an area considered sufficiently large to provide long-term population viability (Rodrigues et al., 2004). For range types with <1000 km² of area available, the entire range area was required to be in the final solution. To provide solutions with a small, but significant, aggregation signal, an outer boundary length penalty ($blm = 0.1$) was defined in the objective function. The best 10 solutions (“add_top_portfolio”) with a low suboptimality gap requirement ($gap = 0.01$ [i.e., the value of solutions needed to be, at most, 1% suboptimal]) were recorded. Solutions were generated using the Gurobi 9.5.0 mixed integer programming solver toolkit (Gurobi Optimization, location) (R code is in Appendix S23).

TABLE 1 Characterization of species' range sections by their adaptive value and conservation potential

Range type	Definition	Dispersal dependence	Conservation role
Full refugia	areas presently occupied by a species that will have continuous climatic suitability over time	none	ideal case in which management is undertaken with high stability and less exposure to uncertain responses to environmental shifts
Partial refugia	areas with climatic suitability for a species in two consecutive periods	none	depending on the temporal discreteness of analyses, management measures may be stable but over less time than full refugia; if outside dispersal window of a species, then assisted colonization should be considered
Leading areas	climatically suitable and potentially occupied areas (given dispersal constraints) in time t that act as source areas for dispersal into climatically suitable areas in $t+1$; may or may not coincide with either full or partial refugia	constrained	areas incorporate transitional value for spatial adaptive processes; management needs to be scheduled for an effective delivery of results; ideally, protection or restoration of these areas in advance allows for their full functionality; measures need to promote high dispersal success
Colonizing areas	climatically suitable areas in time $t+1$ at a dispersal range from occupied areas in t , where populations are likely to settle in; may or may not coincide with full or partial refugia	constrained	areas that incorporate transitional value for spatial adaptive processes; management needs to be scheduled for an effective results; ideally, protection or restoration in advance allows full functionality; measures need to promote high colonization success
Gap areas	areas that are not climatically suitable but occur at a dispersal range from leading and colonizing ranges in time t and $t+1$, respectively	constrained	areas not climatically suitable or occupied by the species; may be used if active local-scale management is implemented; serve transient roles as leading or colonizing areas, but not as much as permanent areas of conservation; may also be sites where assisted colonization is promoted

The Iberian landscape was characterized using multiple factors depicting different mechanisms acting either as resistors of species adaptive dispersal or as sources of uncertainty. The resistance factors were proximity to water ways, predicted evolution of soil moisture, habitat of sufficient quality for species, and topographic complexity. Uncertainty sources were derived from climate projections in two ways: identification of areas with novel climates in future periods and accounting for predictive uncertainty based on frequency selection (among GCMs and model types) of areas as climatically suitable for each species. Only this latter factor varied at a species basis (Appendix S12).

Proximity to water ways

Amphibian species are highly sensitive to water availability; therefore, the occurrence of large extents of water ways close to amphibian populations may determine directly or indirectly (through local meteorological effects) their viability. Using ArcGIS software and data obtained from the European Catchments and Rivers Network System (<https://www.eea.europa.eu/data-and-maps/data/european-catchments-and-rivers-network>), the total length of rivers in each 1×1 km grid cell was recorded. I assumed that the larger the length of rivers inside a grid cell were, the more probable amphibian populations were close to water ways.

Soil moisture

Soil moisture is often used as a predictor for amphibian occurrence (Haggerty et al., 2019). I obtained soil moisture data for

2020 and future periods from Ruosteenoja et al. (2018). Briefly, soil moisture near the surface is derived from climate data and soil geomorphology and projected for all of Europe at 0.25° x 0.25° resolution with 24 GCMs for 1961–2005 and on a yearly basis up to 2099. I used the summer months' (JAS) values to determine the evolution of soil moisture (in percentage from the historical period) under RCP 8.5 (to better align with the SSP585 CMIP6 scenario used in bioclimatic models). Average values for the 2041–2060 and 2061–2080 periods were used to align with the bioclimatic modeling periods of time.

Viable habitat

Habitat characterization was based on the most recent CORINE Land Cover data set (CLC 2018: <https://land.copernicus.eu/pan-european/corine-land-cover/clc201>). With the exception of artificial areas, sclerophyllous vegetation, beaches, sands, burned and saline areas, all remaining land-use classes were assumed to provide habitat for amphibian populations.

Topographic complexity

Topographic complexity measures the variability of elevations in each grid cell. Elevation data were obtained from a digital elevation model built through bilinear interpolation at a 25-m resolution (EU-DEM 1.1: <https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem>). Topographic complexity reflects the standard deviation of

elevations inside each grid cell and was produced using the ArcGIS function Zonal Statistics. The grid cells with the largest elevation variability potentially carry a more diverse array of habitats and climate conditions. They, therefore, offer microscaled opportunities for species to find conditions distinct from the average climate conditions in grid cells.

Nonanalogue climate

Future nonanalogue climates corresponded to particular combinations of climatic variables that were not found either in past or current periods. These constitute climate spaces where the responses of species are highly uncertain and where the predictive performance of bioclimatic models cannot be assessed accordingly. Based on the three climate variables used in the bioclimatic modeling, regions with nonanalogue climates are those whose points in the climate space fall outside the largest convex hull defined by all the climate data for the baseline period (i.e., 2020). This analysis was undertaken for each combination of the two future periods and 10 GCMs. The frequency (from 0 to 20) with which each grid cell possessed a nonanalogue climate was recorded (R code in Appendix S23).

Variability of predictions from bioclimatic modeling

Under an ensemble forecasting framework, the predicted agreement among the GCM and combinations of tested model types is an important indicator of the robustness of the predicted climate suitability patterns for a species in the future. Contrary to all the other factors, this is the only one that was assessed at the species level. For each species, the variance of the AUC-weighted average obtained from the continuous climatic suitability scores (i.e., previous to binary thresholding) was attained by assessing all combinations of the 11 model types and 10 GCMs for 2050 and 2080. An overall value of predictive variability was then appraised based on the highest score obtained in each grid cell for 2050 and 2080 (R code in Appendix S23).

Climate adaptive connectivity

To get an idea of how much the Iberian landscape facilitates climate-adaptive dispersal movements of amphibian species, a resistance layer was generated based on the previously defined factors. For each species, a 0–1 normalization was undertaken for each of the factors, and the final resistance score was defined as an average of the six factors. Because the existence of habitat was assumed to be the most local limiting factor for the occurrence of an amphibian species, the areas with no viable habitat received the largest resistance score possible, irrespective of the remaining factors (i.e., resistance = 1) (Appendix S13).

The value of a landscape matrix to provide connectivity for a species depends largely on how resistant to dispersal the landscape is and how far a species needs to move between habitat

patches (i.e., where populations of a species are likely to persist). I used an area prioritization protocol to determine the habitat patches that would provide suitable conditions at the least cost. For each species, habitat patches were made up of grid cells obtained in the best prioritization solution. For the sake of redundancy, the grid cells selected in >5 runs (out of 10) were also included (Appendix S14). To express close proximity between grid cells highlighted from the area prioritization approach, I assumed grid cells <3 km apart were part of the same habitat patch. In this way, the area of each habitat patch increased and the number of patches to connect decreased.

The value of Iberian grid cells to connect the habitat patches of each species was assessed using Circuitscape 4.0 (McRae & Shah, 2011). Habitat patches defining the focal nodes and the landscape resistance layer corresponded to the input resistance data. In Circuitscape, relationships between resistance and current and voltage are used to simultaneously evaluate the contributions of multiple pathways in each grid cell (McRae et al., 2008). The all-to-one circuit mode was chosen to provide balanced results in terms of quality of analysis and computational timing. For each species, a cumulative layer of conductance values was generated based on the summing of the current originated from all nodes that flowed into each node.

Complementing the overall landscape connectivity layer, the single trajectories of minimum cost linking all the habitat patches (minimum spanning tree in graphs) were identified using the cost connectivity function in ArcGIS over the resistance layer created in Circuitscape.

The cumulative value of landscapes to support adaptive range displacements for all analyzed species was obtained in two ways. First, I summed the 27 aggregated conductance scores delivered by Circuitscape, which favors the connectivity scores of the species with the most discrete habitats prioritized. Second, the conductance values for each species were 0–1 normalized and summed. With this metric landscape, connectivity was assessed homogeneously among species.

Analyses were conducted at the basin scale with the level-5 classification data from HydroSHEDS (Lehner et al., 2006), which allowed the delineation of 16 river basins (Appendices S11 & S21).

Landscape resistance values, conductance scores, and the number of species in patches prioritized in protected areas were compared with the same values in unprotected Iberian lands with Mann–Whitney *U* tests from the `wilcox.test` function in the `stats` R package.

To summarize the adaptive performance of species with respect to the multiple factors assessed (based on range type area, protected area coverage, and landscape connectivity), a principal component analysis was conducted in the `prcomp` function in R `stats`.

RESULTS

In general, the selected climatic variables described the current ranges of species reasonably well. Ensemble models had omission error rates below 0.10 (Appendix S1).

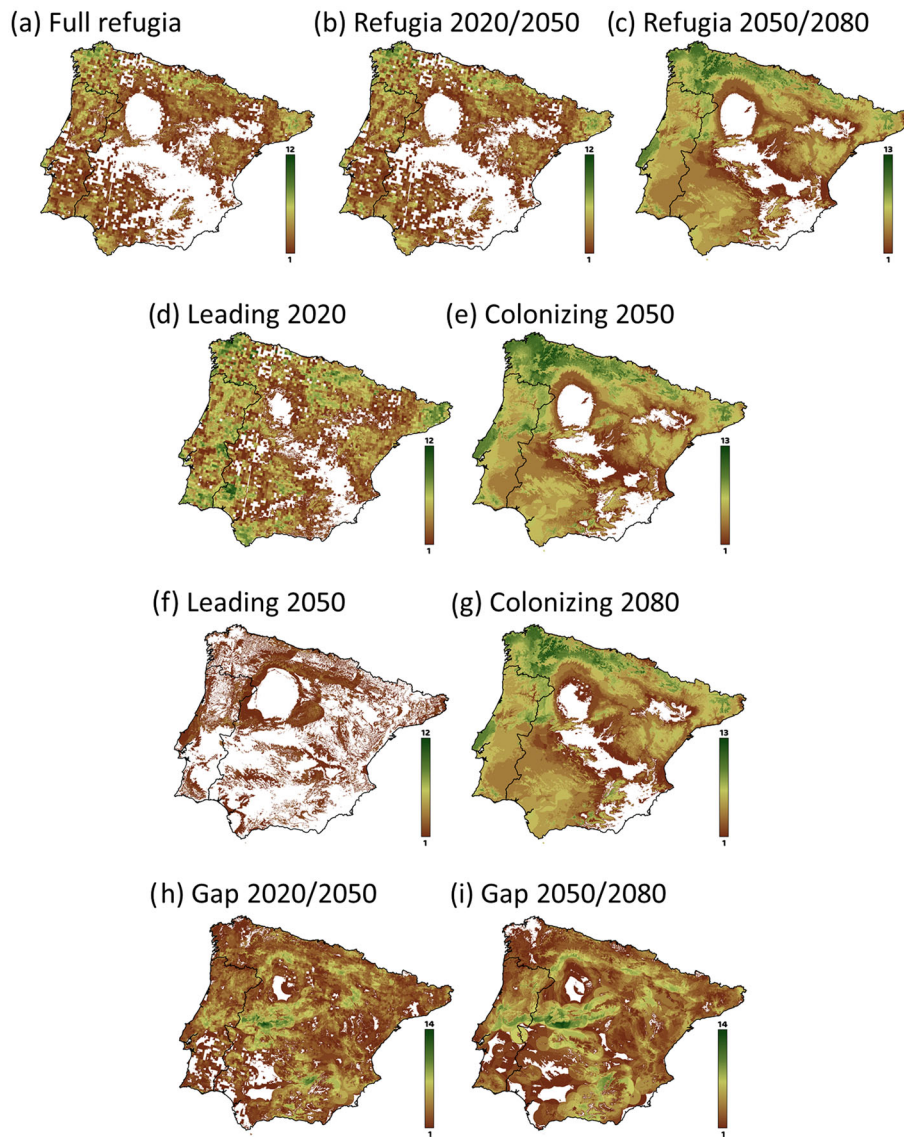


FIGURE 2 Predicted distribution of adaptive range types for 27 species of amphibians responding to climate change in the Iberian Peninsula: (a) full refugia; (b) partial refugia stable from 2020 to 2050; (c) partial refugia stable from 2050 to 2080; (d) leading areas in 2020; (e) colonizing areas in 2050; (f) leading areas in 2050; (g) colonizing areas in 2080; (h) gap areas from 2020 to 2050; and (i) gap areas from 2050 to 2080. Types of areas (e.g., full refugia) are defined in Table 1

Geographic basis

Full refugia for the largest number of species occurred predominantly in coastal regions of the Iberian Peninsula, particularly in the northwest, in a large longitudinal stripe in the north, the Catalonia region, and in the south along Cadiz and Malaga (Figure 2). The northwest and most western regions were also predicted to be of particular value for climate-driven colonization areas for 2050 and 2080. A general bottleneck emerged in 2050. Very small functional areas were available in leading areas, and when they did occur, they could only support a few species. This showed the critical conservation value of the very small and scattered leading adaptive areas. These were relevant for a large number of species and served as leading grounds for dispersal processes. A large fraction in the center of the peninsula was predicted to be unsuitable for most of the amphibians

through time because it lacked refugia, leading, and colonizing areas. However, this central zone accommodated gap areas for several species.

At the river basin scale, the full climatic refugia for the 27 species covered >60% of the basins along the Atlantic coast and in the southeast. With time, the species ranges of the 27 species got less coincident at the river basin level (Appendices S8, S9, S16, & S17). The bottleneck effect evidenced in the low representativeness of leading areas in 2050 was replicated at the river basin level, and its magnitude was expressed in a latitudinal gradient of basin coverage; the northernmost basins contained the largest coverages of 2050 leading areas.

Generally, the areas highlighted for the protection of the climate adaptive range types for the 27 amphibian species were scattered throughout most of the Iberian Peninsula. No priority areas were highlighted in the most central part of the

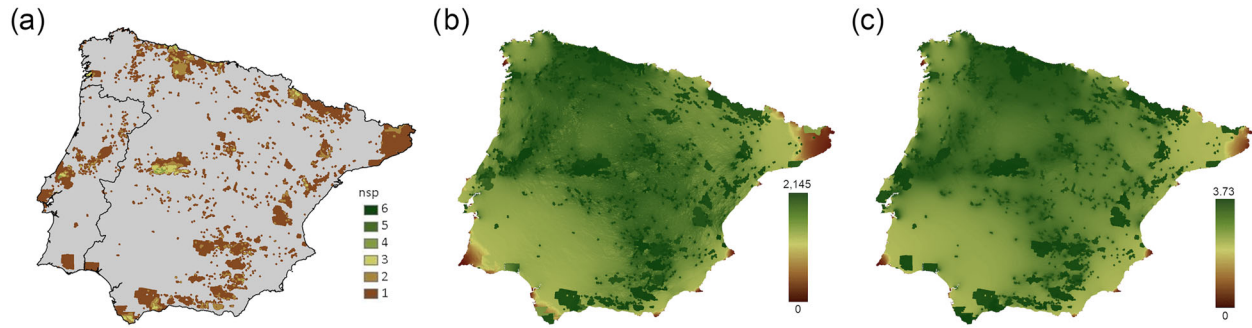


FIGURE 3 The climate adaptive range areas (a) prioritized for conservation (nsp, number of species favored by the protection of a grid cell) and associated landscape connectivity, (b) sum of connectivity patterns among species (0–2145), and (c) sum of standardized connectivity patterns among species (0–3.73).

region (Figure 3). A few small areas were valuable for up to six species (very localized regions in the north), but extensive areas valuable for 3–4 species followed several mountain ranges in the west (Serra de Aire e Candeeiros), northwest (Cordillera Cantabria), west Pyrenees and the Betic Chain; and coastal region of Andalusia. Because landscape conductance closely followed the density of areas to link, these same regions had the largest adaptive conductance scores.

In general, protected areas appeared well located to facilitate the adaptive movement of species up to 2080. Resistance values in protected areas were significantly lower ($U = 4.9e10$; $p < 0.001$) than friction values in unprotected areas. Complementarily, conductance ($U = 4.7e10$; $p < 0.001$) and species richness in prioritized patches ($U = 4.6e10$; $p < 0.001$) were significantly higher inside protected areas than outside (Appendix S22).

Species basis

Between 2050 and 2080, only *Bufo bufo* and *Rana perezi* occupied almost all their available suitable range by 2020 (Figure 4). For three species, large negative biases were predicted in the occupancy of climatically suitable areas (*Discoglossus pictus*, *Rana dalmatina*, and *Rana pyrenaica*). For most of the species, these occurrences to potential occurrence equilibrium ratios were maintained inside and outside protected areas (Appendices S5–S7).

All species had very small colonizing areas by 2050 at a functional dispersal distance from the baseline range (Figure 4). This was particularly marked for *Alytes dickbilleni* (11% potentially suitable range area by 2050), *R. dalmatina* (12%), *D. pictus* (18%), and *R. pyrenaica* (22%). For these species, by 2050 their functional leading adaptive areas were also particularly small. The most extreme case was for *R. dalmatina*. It had only a small leading area in 2050. However, an abrupt reduction in leading range area by 2050 was predicted for most species because large distances between colonizing areas in 2050 and climatically suitable areas in 2080 were predicted.

The amount of climatically suitable colonizing area declined from 2020 to 2080; the largest decreases were predicted for *Alytes cisternasii* (42% of 2020 area), *Alytes obstetricans* (62%), *R.*

perezi (74%), *Pelodytes punctatus* (76%), and *A. dickbilleni* (80%). Contrarily, for half the species, colonizing areas in 2080 were significantly larger than occurrence areas in 2020.

Chioglossa lusitanica, *Discoglossus galganoi*, *Hyla meridionalis*, *Pelodytes ibericus*, and *Rana iberica* had more than 90% of their current occupied areas continuously preserved climatically until 2080 (full refugia). For most of the species, the relative occupancy of full refugia was maintained inside and outside protected areas (Appendices S5–S7).

For *R. pyrenaica*, *R. dalmatina*, and *P. ibericus*, the 1000-km² protection target was not achieved for at least one adaptive range type. The latter two species had very small suitable leading areas available in 2050 (Figures 3 & 4). For *Euproctus asper*, *Lissotriton helveticus*, *P. ibericus*, and *R. perezi*, the range areas to prioritize for conservation covered <4000 km². In general, the climate adaptive range areas of most species were in the northernmost river basins (Norte, Duero, Ebro, and Onyar) (Appendix S16). Except for *P. ibericus*, the species with the largest full refugia areas were not the ones with the lowest area prioritized for protection (Appendix S15).

The highest average standardized resistance values were for *Hyla arborea* (0.74), *Bufo calamita* (0.71), *A. cisternasii* (0.70), *Triturus marmoratus* (0.70), and *D. galganoi* (0.70). Average friction of *R. perezi* was the lowest (0.55). *Lissotriton boscai* had the lowest friction value (0.11). In general, friction scores were equally distributed among species' range sections (Appendices S18 & S19).

A. obstetricans, *B. bufo*, and *R. perezi* had the largest positive deviances of conductance scores from an expected value for species with a similar extent of area and number of patches to prioritize (Appendix S20). At the other extreme, the very low conductance scores for the adaptive movements of *R. pyrenaica* deviated greatly from the expected for a species with the same total area and the number of patches needed for protection. With the exception of *R. iberica*, the species with large numbers of patches (>60) had smaller conductance hotspot areas than expected for species with the similar area and the number of patches prioritized. In contrast, *H. arborea*, a clear outlier, had a conductance hotspot area much higher than expected for species with a similar surface area and the number of patches prioritized. Maps of landscape conductance and minimum spanning tree connectivity of each species are in Appendix S10.

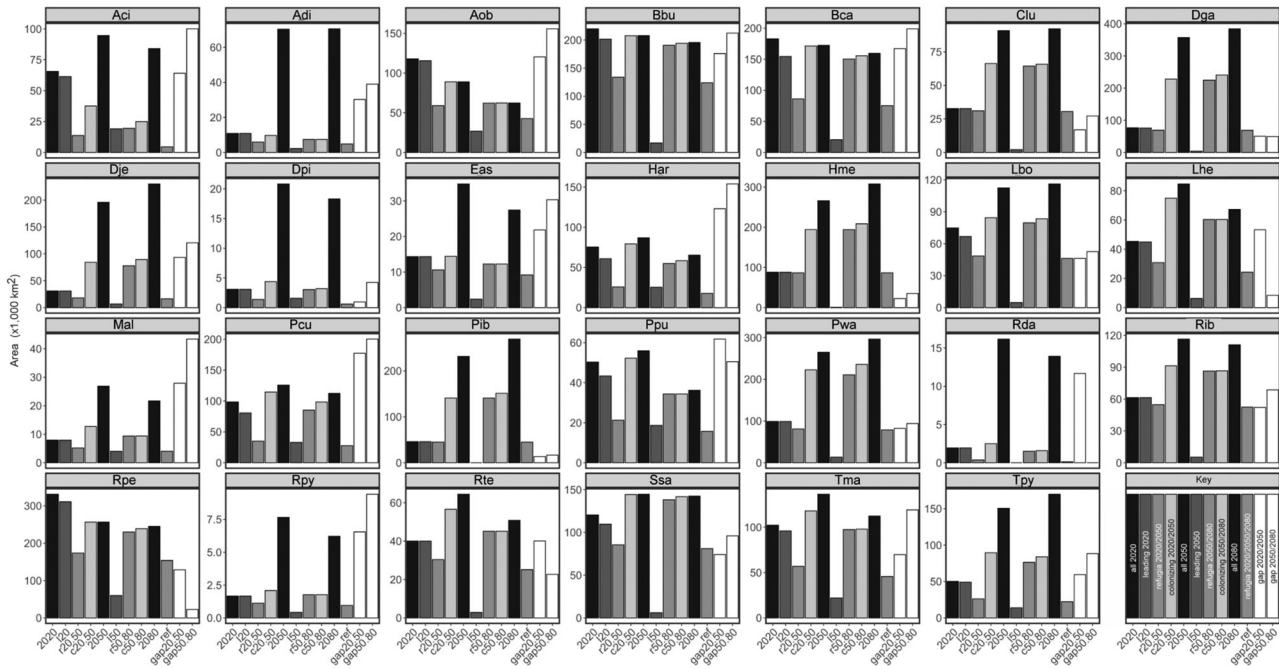


FIGURE 4 Total area associated with each climate adaptive range type: occurrence range in the baseline period (2020); range of populations in the baseline period at an effective dispersal distance from climatically suitable areas in 2050 (l20); occurrence areas in the baseline period with suitable climate in 2050 (r20.50); climatically suitable areas in 2050 potentially at an effective dispersal distance from occurrence areas in the baseline period (c20.50); climatically suitable areas in 2050 (2050); populations in colonizing and refugia 2020–2050 at an effective dispersal distance from climatically suitable areas in 2080 (l50); areas in 2050 that maintain climate suitability in 2080 (r50.80); climatically suitable areas in 2080 potentially at an effective dispersal distance from the colonizing and refugia 2020–2050 (c50.80); climatically suitable areas in 2080 (2080); stable refugia maintaining climatic suitability from the baseline period to 2080 (ref); areas with no suitable climate in the baseline period and 2050 but at dispersal distance from occurrence areas in 2020 and the colonizing 2020–2050 range (gap20.50); areas with no suitable climate in 2050 and 2080 but at dispersal distance from colonizing ranges in 2020–2050 and 2050–2080 (gap50.80) (Aci, *Alytes cisternasii*; Adi, *Alytes dickhilleni*; Aob, *Alytes obstetricans*; Bbu, *Bufo bufo*; Bca, *Bufo calamita*; Clu, *Chioglossa lusitanica*; Dga, *Discoglossus galganoi*; Dje, *Discoglossus jeanneae*; Dpi, *Discoglossus pictus*; Eas, *Euproctus asper*; Har, *Hyla arborea*; Hme, *Hyla meridionalis*; Lbo, *Lissotriton boscai*; Lhe, *Lissotriton belgicus*; Mal, *Mesotriton alpestris*; Pcu, *Pelobates cultripes*; Pib, *Pelodytes ibericus*; Ppu, *Pelodytes punctatus*; Pwa, *Pleurodeles waltl*; Rda, *Rana dalmatina*; Rib, *Rana iberica*; Rpe, *Rana perezi*; Rpy, *Rana pyrenaica*; Rte, *Rana temporaria*; Ssa, *Salamandra salamandra*; Tma, *Triturus marmoratus*; Tpy, *Triturus pygmaeus*)

DISCUSSION

Understanding range shifts from a biogeographical perspective is essential for informing a changing-paradigm conservation science and for designing conservation strategies that are resistant, resilient, and facilitative of adaptation to climate change. I explored the utility of an analytical framework to pinpoint the time-varying patterns of spatial adaptive responses of species to climate change. The areas identified and their specific functional timings provide useful guidelines for the scheduling of management actions concerning each adaptive stage.

My results reinforce the urgency for conservation and restoration measures to improve landscape condition and connectivity for Iberian amphibian species and thus reduce extinction debts (Araújo et al., 2006; Rodríguez-Rodríguez et al., 2020a; Scroggie et al., 2019). Most of the species had small leading grounds to disperse from 2050 to 2080 relative to the size of the other range areas. This pattern resulted from the interplay of two mechanisms. First, for some species, suitable colonization areas in 2050 were already small, thus providing small space for leading areas to exist. Second, the high velocity of climate change increased the distance between colonizing areas in 2080

from range areas in 2050, leaving less space for leading areas in 2050 at a functional dispersal range. Although this bottleneck effect was not predicted to undermine the persistence of species (given the increase of colonizing area by 2080), it may still underline the need for assisted colonization plans, at least for the most affected species (e.g., *R. dalmatina*).

The classification of species according to the adaptive factors evaluated indicated that the species that had the largest occurrence areas in 2020 in protected areas were also the species that had the lowest fraction of climatically suitable colonizing areas in 2050 and 2080 (Figure 5). This negative correlation between both factors means that species whose 2020 ranges are secure in protected areas will be the same species that in the future time will have the fewest colonizing areas available, thus reflecting an impoverishment of their expected persistence in the Iberian Peninsula. This was particularly evident for *A. dickhilleni*, *R. pyrenaica*, *A. cisternasii*, *D. pictus*, and *R. dalmatina*. The second PCA axis showed an inverse relationship between occurrence areas by 2020 and the size of colonizing areas in 2080. The latter three of the above-mentioned species are particularly vulnerable in this respect, and they had the largest adaptive area to prioritize because of the low geographic overlap of their adaptive range

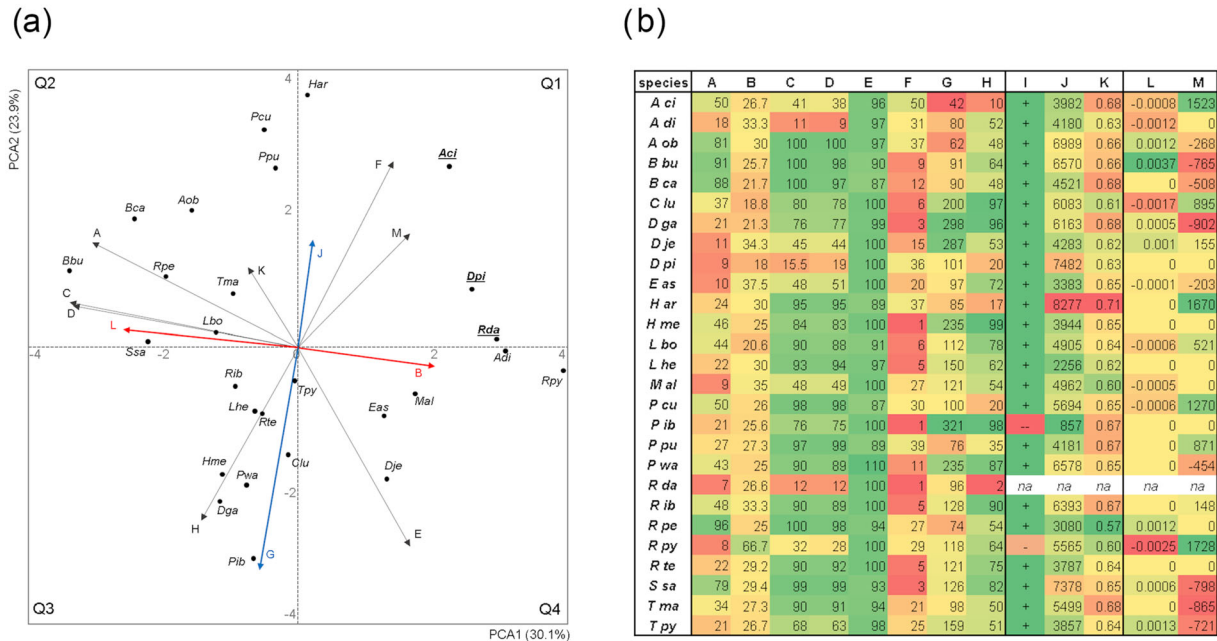


FIGURE 5 (a) Principle component analysis (PCA) defining an analytical space used to prioritize species protection based on species' adaptive performance under climate change (red arrows, factors with the largest variability explained in the first PCA axis; blue arrows, factors with the largest variability explained in the second PCA axis; Q1, Q2, Q3, and Q4 are quadrants of the analytical space) and (b) performance of the amphibian species for 13 evaluation indices (A–M) based on their climate adaptive capabilities in the Iberian Peninsula (colors, adequacy of species performance under each factor in a gradient from worst performing [dark red] to best performing [dark greens]; na, not assessed; species abbreviations, defined in the legend of Figure 4; A, percentage of potential climatically suitable areas in the baseline period occupied by the species; B, percentage of occupied areas in the baseline period in protected areas; C, percentage of predicted climatically suitable areas in 2050 with colonizing-prone areas; D, percentage of predicted climatically suitable areas in 2080 with colonizing prone areas; E, percentage of occurrence areas in the baseline period available as sourcing grounds of populations toward climatically suitable areas in 2050 [leading 2020]; F, percentage of colonizing areas in 2050 available as sourcing grounds of populations toward climatically suitable areas in 2080 [leading 2050]; G, percentage of total area of occurring ranges in baseline period against predicted colonizing area by 2080, H, percentage of occurring areas in the baseline period predicted to maintain climatic suitability up to 2080 [full refugia]; I, feasibility of 1000 km² range section representation targets; J, total area [km²] selected as the minimum area representing adequately adaptive range section at 1000 km²; K, average friction values of the areas selected [compared with the average friction among species, 0.64]; L, absolute deviance of conductance levels from the interval of confidence obtained after regressing conductance with the amount of areas selected and number of patches; M, absolute deviance of conductance hotspot area from the interval of confidence obtained after regressing conductance with the amount of areas selected and number of patches). In factors A–H, the neutral performance value is 30% (yellow) because it defines the area target identified for protection by 2030 (Convention of Biological Diversity)

types with time. *A. cisternassi*, *D. pictus*, and *R. dalmatina* emerged as the species with the least adaptability to the predicted climate change in the Iberian Peninsula, and their persistence is largely reliant on the effectiveness of conservation measures.

There is a wide set of options for the conservation of species presenting significant climate-driven range shifts (Krosby et al., 2010; Littlefield et al., 2019; McGuire et al., 2016), including measures to bolster resistance, resilience, and facilitative adaptation to climate change. Resistance actions can overcome the effects of small levels of climate change or, when climate velocity is high, save native species in the short term until other options are available (gap zones in Table 1). Resistant strategies may include increasing water supply through small manipulations of hydrological flows or moisture regimes; filling of natural or artificial ponds; amelioration of irrigation systems; establishment of naturalized fountains in urban or semiurban gardens or sprinkler systems to retain surface moisture; improving soil permeability; and watering vegetation well to provide enduring moisture conditions necessary for amphibian life-cycles (Shoo et al., 2011). The occupation of the Iberian Peninsula by Moors 2000 years ago left a wide array of water reservoir infrastructures

in small urban and periurban settlements that might have been essential for the persistence of amphibians by that time and that may be important for the persistence of the species now and in the future. The eradication of invasive species, such as the common water hyacinth (*Eichhornia crassipes*), red swamp crayfish (*Proclarkia clarkii*), and largemouth bass (*Micropterus salmoides*) (very pervasive in freshwater systems in the Iberian Peninsula) (Anastácio et al., 2019; Falaschi et al., 2020), and the control of disease outbreaks are central actions to take into account (Rosa et al., 2017).

Resilience strategies provide the means for species' populations to recover from disturbances (here climate change). The restoration of degraded ecosystems, particularly rivers and ponds, may enlarge the suitable areas needed for amphibian species to endure. The legal protection of wetlands and other habitats considered to maintain amphibian populations viability under climate change may provide the means for systems to self-regulate. Preferably, those areas should encompass a rich mosaic of habitats and high physiographic diversity, involving vegetation systems that preserve cool and wet regimes, north-facing slopes, and depressions, which function as climatic

refugia (Hannah et al., 2014; Lenoir et al., 2017). In the Iberian Peninsula, water transfers are already being made from rivers in the northern basins to southern ones to attenuate the increasing dryness of southern river systems in summer. Judicious and controlled water transfers may still be a positive management option for several amphibian species' populations to persist in the south. However, these highly artificial interventions along river courses may facilitate the flow of invasive species and pathogens that may add another layer of threat to climate change.

The longer periods of dryness predicted for the upcoming years may lead to more aggressive and intensive agriculture practices. The excessive use of water and fertilizers may interact with climate change to stress amphibian populations (Egea-Serrano & Van Buskirk, 2016). Thus, incentives to make agriculture production more environmentally friendly are requested in national and European policies. The new European Common Agriculture Policy goes in this direction (see: https://ec.europa.eu/info/food-farming-fisheries/key-policies/common-agricultural-policy/new-cap-2023-27_en).

The genetic dimension may require action to provide resilience to amphibian populations. Preserving genetic diversity of peripheral populations, where genotypes may be better adapted to climatic stressors (i.e., the leading grounds considered in the present study), is likely to boost future adaptation potential (Razgour et al., 2019). In some cases, for the sake of rational conservation investment, some populations on the verge of extinction might be left on their own, whereas conservation resources are invested in populations that might more successfully endure in the long term (Wiedenfeld et al., 2021). My results identify, for each species, areas that appear best suited to provide such adaptive areas up to 2080.

Facilitative interventions are those best aligned with the aim of this study because it provides guidance on where and when to invest to increase the success of the natural adaptive processes of species by means of climate-driven dispersal and colonization mechanisms (Robillard et al., 2015). The areas providing the best chances of adaptation need to be managed actively, and the habitat therein is made functional for amphibian species. For some populations to persist, assisted colonization may be the only mechanism for providing functional grounds outside the natural dispersal window (Gallagher et al., 2015; McLachlan et al., 2007). Based on my results, the leading, colonizing, and refugia areas that were not prioritized still offer, at particular life-history stages, conditions that provide seed populations of amphibian species. These same interventions may also be carried out in gap regions (but, given their unsuitable climatic conditions, may need more active management measures) because of their strategic location within a dispersal range from climatically suitable areas. In any case, assisted colonization needs to be accompanied by a full screening of their effects on the entire ecosystem.

For the sake of efficiency and effectiveness, this repertoire of options is to be undertaken preferably in the leading, colonizing, and refugia areas pinpointed in the prioritization protocol because the connectivity assessment made here uses those areas as central nodes of a coherent network of sites on which to focus conservation. My framework provides the times when

those measures are most and least relevant and, therefore, provides a dynamic protocol with which to identify areas for intervention. Full refugia are, by their nature, where actions may be planned for the long term.

As for any other conservation plan undertaken at the biogeographical level, these analyzes come with several caveats. First, species distribution data based on different correlative models and GCMs are inherently uncertain (Araújo et al., 2019). At the biogeographical scale I used to calibrate the models, the climate is one of the most limiting factors to consider (Pearson & Dawson, 2003). At the small scale of 1 km² (i.e., predictive resolution), there were other factors that would need consideration in more detailed assessments (e.g., vegetation type, soil properties, and water availability). It is important to emphasize that the resistance layers accounted for the multi-model and GCM variability of suitability predictions for each species through time and for the occurrence of novel climates where model performance was barely validated (Williams et al., 2007).

Second, in my analyses, species interactions were not considered. The effect of novel communities emerging from climate change would add another layer of uncertainty to the way amphibians respond in the future (Ordóñez et al., 2016; Pandolfi et al., 2020). Third, a general account of species' dispersal abilities relative to dispersal velocity and landscape effect would lead to better estimates of the amount of the different species' range areas (McCauley & Mabry, 2011). This shortfall was partially overcome with the use of a landscape-based resistance layer when assessing the landscape connectivity value in facilitating climate-driven range shifts (Keeley et al., 2018; Keeley et al., 2021). Fourth, finer temporal-resolute predictions of landscape characteristics in the future (i.e., more periods of time assessed) would better align with the future predictions of species' range shifts. Fifth, in cost-effective conservation plans, a large number of species encompassing different taxonomic and functional groups are usually considered. Therefore, in a putative follow-up to this study, area prioritization assessments would be better performed for a set of species instead of for the areas that, at a species level, identify optimal areas relative to costs and benefits. Indeed, more context-specific work at higher resolutions would be needed to support decision-making (Sykora-Bodie et al., 2021).

Several metrics of adaptive success were chosen to cover a wide set of plausible geographical response modes. Several could have been used if data were available (Oldfather et al., 2020). Of particular interest to examine would be metapopulation dynamics, effective population abundance, and genetic diversity of populations. These factors would provide more details about the adaptability of species at very local scales and, therefore, could guide more specific management actions. For example, the poor genetic diversity of some populations in the leading edges could be compensated for with the introduction of alleles considered more adaptive in the face of climate change (Shoo et al., 2013; Weeks et al., 2011). Also, the identification of connectivity flows in a metapopulation structure would lead to prioritizing connected areas for protection and to managing them based on expected local climatic shifts (e.g., through

engineering schemes or persistent nature-based solutions as artificial ponds with controlled water quality and availability) (Campbell-Grant et al., 2010). Several studies report niche differentiation among some of the studied species (Martínez-Gil et al., 2021; Rodríguez-Rodríguez et al., 2020b). Ideally, when data exist, specific minimum area requirements and connectivity properties would be defined for each of the individual populations, so as to conserve the variability of local species' adaptations in a risk-averse portfolio approach. The abundance of species could be used to identify possible extinction debts, which cannot be obtained from binary occurrence data (Peterson et al., 2019). These debts outline natural states of decline that need to be urgently identified and reversed (Fordham et al., 2016). Population abundance also informs the magnitude of the dispersal flows of individuals.

There are no easy answers to the current biodiversity crisis, and actions may be costly. However, safeguarding basal trophic groups in ecosystems, such as amphibians, may potentiate ecosystem functionality and multiply by several factors the benefits of financial investments in conservation. The design of highly beneficial policies implies the use of dedicated spatial conservation models that rely on optimization frameworks to determine where, when, and what should be done to preserve at minimum cost the adaptive potential of species and the functioning of the ecosystems that depend on them.

ACKNOWLEDGEMENTS

This research was funded by national funds through the Fundação para a Ciência e a Tecnologia (FCT) under the project UIDB/05183/2020. I am grateful to V. Bastazini (University of Évora) for his support in revising the manuscript, P. Sá Sousa (University of Évora) for seminal discussions of the study, and the association Almargem (<http://almargem.org/site/>), which challenged me to undertake the study. I also acknowledge three anonymous reviewers for their relevant feedback.

ORCID

Diogo Alagador  <https://orcid.org/0000-0003-0710-3187>

REFERENCES

- Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2014). Shifting protected areas: Scheduling spatial priorities under climate change. *Journal of Applied Ecology*, 51, 703–713.
- Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2016). Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. *Methods in Ecology and Evolution*, 7, 853–866.
- Anastácio, P. M., Ribeiro, F., Capinha, C., Banha, F., Gama, M., Filipe, A. F., Rebelo, R., & Sousa, R. (2019). Non-native freshwater fauna in Portugal: A review. *Science of the Total Environment*, 650, 1923–1934.
- Araújo, M. B., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., García, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, 5, eaat4858.
- Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22, 42–47.
- Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A., Valdes, P. J., & Rahbek, C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, 31, 8–15.
- Araújo, M. B., Thuiller, W., & Pearson, R. G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33, 1712–1728.
- Ascensão, F., D'Amico, M., Martins, R. C., Rebelo, R., Barbosa, A. M., Bencatel, J., Barrientos, R., Abellán, P., Tella, J. L., Cardador, L., Anadón, J. D., Carrete, M., Murgui, E., Fernandes, P., Santos, S. M., Mira, A., Mathias, M. D. L., Tiago, P., Casabella, E., ... Capinha, C. (2021). Distribution of alien tetrapods in the Iberian Peninsula. *NeoBiota*, 64, 1–21.
- Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18, 1866–1879.
- Campbell-Grant, E. H., Nichols, J. D., Lowe, W. H., & Fagan, W. F. (2010). Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proceedings of the National Academy of Sciences*, 107, 6936–6940.
- Cardoso Pereira, S., Marta-Almeida, M., Carvalho, A. C., & Rocha, A. (2020). Extreme precipitation events under climate change in the Iberian Peninsula. *International Journal of Climatology*, 40, 1255–1278.
- Carvalho, S. B., Brito, J. C., Crespo, E. J., & Possingham, H. P. (2011). Incorporating evolutionary processes into conservation planning using species distribution data: A case study with the western Mediterranean herpetofauna. *Diversity and Distributions*, 17, 408–421.
- Carvalho, S. B., Torres, J., Tarroso, P., & Velo-Antón, G. (2019). Genes on the edge: A framework to detect genetic diversity imperiled by climate change. *Global Change Biology*, 25, 4034–4047.
- Clancy, N. G. (2017). Can amphibians help conserve native fishes? *Fisheries*, 42, 327–331.
- de Vries, W., Marco, A. J. B., & Herpetology, A. (2017). The importance of fluvial habitats for amphibian conservation in the Mediterranean climate. *Basic and Applied Herpetology*, 31, 5–16.
- Dufresnes, C., & Perrin, N. (2015). Effect of biogeographic history on population vulnerability in European amphibians. *Conservation Biology*, 29, 1235–1241.
- Earl, J. E., Blomquist, S. M., Harper, E. B., Hocking, D. J., Hunter, M. L., Johnson, J. R., Osbourn, M. S., Patrick, D. A., Popescu, V. D., Rittenhouse, T. A. G., & Rothermel, B. B. (2022). Amphibian biomass export from geographically isolated wetlands: Temporal variability, species composition, and potential implications for terrestrial ecosystems. *Diversity*, 14, 163.
- Egea-Serrano, A., & Van Buskirk, J. (2016). Responses to nitrate pollution, warming and density in common frog tadpoles (*Rana temporaria*). *Amphibia-Reptilia*, 37, 45–54.
- Enriquez-Urzelai, U., Kearney, M. R., Niecieza, A. G., & Tingley, R. (2019). Integrating mechanistic and correlative niche models to unravel range-limiting processes in a temperate amphibian. *Global Change Biology*, 25, 2633–2647.
- Falaschi, M., Melotto, A., Manenti, R., & Ficetola, G. F. (2020). Invasive species and amphibian conservation. *Herpetologica*, 76, 216–227.
- Ficetola, G. (2015). Habitat conservation research for amphibians: Methodological improvements and thematic shifts. *Biodiversity and Conservation*, 24, 1293–1310.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Fordham, D. A., Brook, B. W., Hoskin, C. J., Pressey, R. L., VanDerWal, J., & Williams, S. E. (2016). Extinction debt from climate change for frogs in the wet tropics. *Biology Letters*, 12, 20160236.
- Fritz, K. A., & Whiles, M. R. (2018). Amphibian-mediated nutrient fluxes across aquatic–terrestrial boundaries of temporary wetlands. *Freshwater Biology*, 63, 1250–1259.
- Gallagher, R. V., Makinson, R. O., Hogbin, P. M., & Hancock, N. (2015). Assisted colonization as a climate change adaptation tool. *Austral Ecology*, 40, 12–20.
- Gómez, A., & Lunt, D. H. (2007). Refugia within refugia: Patterns of phylogeographic concordance in the Iberian Peninsula. In S. Weiss, & N. Ferrand (Eds.), *Phylogeography of Southern European refugia: Evolutionary perspectives on the origins and conservation of European biodiversity* (pp. 155–188). Dordrecht: Springer.

- Gurobi Optimization Inc. (2018). Gurobi optimizer reference manual. Version 7.5.1.
- Haggerty, C. J. E., Crisman, T. L., & Rohr, J. R. (2019). Effects of forestry-driven changes to groundcover and soil moisture on amphibian desiccation, dispersal, and survival. *Ecological Applications*, *29*, e01870.
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, *29*, 390–397.
- Hanson, J. O., Schuster, R., Morrell, N., Strimas-Mackey, M., Edwards, B. P. M., Watts, M. E., Arcese, P., Bennett, J., & Possingham, H. P. (2022). prioritizr: Systematic conservation prioritization in R. R package version 7.1.1.
- Hocking, D. J., & Babbitt, K. J. (2014). Amphibian contributions to ecosystem services. *Herpetological Conservation and Biology*, *9*, 1–17.
- Keeley, A. T., Ackerly, D. D., Cameron, D. R., Heller, N. E., Huber, P. R., Schloss, C. A., Thorne, J. H., & Merenlender, A. M. (2018). New concepts, models, and assessments of climate-wise connectivity. *Environmental Research Letters*, *13*, 073002.
- Keeley, A. T. H., Beier, P., & Jenness, J. S. (2021). Connectivity metrics for conservation planning and monitoring. *Biological Conservation*, *255*, 109008.
- Krosby, M., Tewksbury, J., Haddad, N. M., & Hoekstra, J. (2010). Ecological connectivity for a changing climate. *Conservation Biology*, *24*, 1686–1689.
- Lehner, B., Verdin, K., & Jarvis, A. (2006). *HydroSHEDS technical documentation*. Washington, DC: HydroSHEDS.
- Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*, 253–266.
- Littlefield, C. E., Krosby, M., Michalak, J. L., & Lawler, J. J. (2019). Connectivity for species on the move: Supporting climate-driven range shifts. *Frontiers in Ecology and the Environment*, *17*, 270–278.
- Loureiro, A., Ferrand de Almeida, N., Carretero, M. A., & Paulo, O. S. (2008). *Atlas dos Anfíbios e Répteis de Portugal*. Lisbon: Instituto da Conservação da Natureza e da Biodiversidade.
- Martínez-Gil, H., Martínez-Freiria, F., Perera, A., Enriquez-Urzelai, U., Martínez-Solano, Í., Velo-Antón, G., & Kaliontzopoulou, A. (2021). Morphological diversification of Mediterranean anurans: The roles of evolutionary history and climate. *Biological Journal of the Linnean Society*, *135*, 462–477.
- McCauley, S. J., & Mabry, K. E. (2011). Climate change, body size, and phenotype dependent dispersal. *Trends in Ecology & Evolution*, *26*, 554–555.
- McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences*, *113*, 7195–7200.
- McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, *21*, 297–302.
- McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution and conservation. *Ecology*, *89*, 2712–2724.
- McRae, B. H., & Shah, V. B. (2011). Circuitscape user guide.
- Miller, D. A. W., Grant, E. H. C., Muths, E., Amburgey, S. M., Adams, M. J., Joseph, M. B., Waddle, J. H., Johnson, P. T. J., Ryan, M. E., Schmidt, B. R., Calhoun, D. L., Davis, C. L., Fisher, R. N., Green, D. M., Hossack, B. R., Rittenhouse, T. A. G., Walls, S. C., Bailey, L. L., Cruickshank, S. S., ... Sigafus, B. H. (2018). Quantifying climate sensitivity and climate-driven change in North American amphibian communities. *Nature Communications*, *9*, 3926.
- Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*, 368–375.
- Oldfather, M. F., Kling, M. M., Sheth, S. N., Emery, N. C., & Ackerly, D. D. (2020). Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. *Global Change Biology*, *26*, 1055–1067.
- Ordóñez, A., Williams, J. W., & Svenning, J.-C. (2016). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change*, *6*, 1104–1109.
- Pandolfi, J. M., Staples, T. L., & Kiessling, W. (2020). Increased extinction in the emergence of novel ecological communities. *Science*, *370*, 220.
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*, 361–371.
- Peterson, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. *Global Change Biology*, *25*, 775–793.
- Pittman, S. E., Osbourn, M. S., & Semlitsch, R. D. (2014). Movement ecology of amphibians: A missing component for understanding population declines. *Biological Conservation*, *169*, 44–53.
- Pleguezuelos, J. M., Márquez, R., & Lizana, Y. M. (2002). *Atlas y Libro Rojo de los Anfíbios y Reptiles de España*. Madrid: Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española.
- Qazi, A. H., & Ashok, K. (2012). Global amphibian declines: A review. *International Journal of Biodiversity and Conservation*, *4*, 348–357.
- R Development Core Team. (2021). R: A language and environment for statistical computing, R Foundation for Statistical Computing (version 4.1.2).
- Razgour, O., Forester, B., Taggart, J. B., Bekaert, M., Juste, J., Ibáñez, C., Puechmaille, S. J., Novella-Fernandez, R., Alberdi, A., & Manel, S. (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proceedings of the National Academy of Sciences*, *116*, 10418.
- Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, *29*, 1586–1595.
- Rodrigues, A. S. L., Akçakaya, H. R., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Chanson, J. S., Fishpool, L. D. C., Fonseca, G. A. B. D., Gaston, K. J., Hoffmann, M., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., ... Yan, X. (2004). Global gap analysis: Priority regions for expanding the global protected-area network. *BioScience*, *54*, 1092–1100.
- Rodríguez-Rodríguez, E. J., Beltrán, J. F., El Mouden, E. H., Slimani, T., Márquez, R., & Donaire-Barroso, D. (2020a). Climate change challenges IUCN conservation priorities: A test with western Mediterranean amphibians. *SN Applied Sciences*, *2*, 216.
- Rodríguez-Rodríguez, E. J., Beltrán, J. F., Tejado, M., Nicieza, A. G., Llusia, D., Márquez, R., & Aragón, P. (2020b). Niche models at inter- and intraspecific levels reveal hierarchical niche differentiation in midwife toads. *Scientific Reports*, *10*, 10942.
- Rosa, G. M., Sabino-Pinto, J., Laurentino, T. G., Martel, A., Pasmans, F., Rebelo, R., Griffiths, R. A., Stöhr, A. C., Marschang, R. E., Price, S. J., Garner, T. W., & Bosch, J. (2017). Impact of asynchronous emergence of two lethal pathogens on amphibian assemblages. *Scientific Reports*, *7*, 43260.
- Rovito, S. M., Parra-Olea, G., Vásquez-Almazán, C. R., Papenfuss, T. J., & Wake, D. B. (2009). Dramatic declines in neotropical salamander populations are an important part of the global amphibian crisis. *Proceedings of the National Academy of Sciences*, *106*, 3231–3236.
- Ruosteenoja, K., Markkanen, T., Venäläinen, A., Räisänen, P., & Peltola, H. (2018). Seasonal soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st century. *Climate Dynamics*, *50*, 1177–1192.
- Scroggie, M. P., Preece, K., Nicholson, E., McCarthy, M. A., Parris, K. M., & Heard, G. W. (2019). Optimizing habitat management for amphibians: From simple models to complex decisions. *Biological Conservation*, *236*, 60–69.
- Shoo, L. P., Hoffmann, A. A., Garnett, S., Pressey, R. L., Williams, Y. M., Taylor, M., Falconi, L., Yates, C. J., Scott, J. K., Alagador, D., & Williams, S. E. (2013). Making decisions to conserve species under climate change. *Climatic Change*, *119*, 239–246.
- Shoo, L. P., Olson, D. H., McMenamin, S. K., Murray, K. A., Sluys, M. V., Donnelly, M. A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S. M., Bishop, P. J., Corn, P. S., Dovey, L., Griffiths, R. A., Lowe, K., Mahony, M., McCallum, H., Shuker, J. D., Simpkins, C., ... Hero, J.-M. (2011). Engineering a future for amphibians under climate change. *Journal of Applied Ecology*, *48*, 487–492.
- Sillero, N. (2021). Climate change in action: Local elevational shifts on Iberian amphibians and reptiles. *Regional Environmental Change*, *21*, 101.
- Speybroeck, J., Beukema, W., Dufresnes, C., Fritz, U., Jablonski, D., Lymberakis, P., Martínez-Solano, I., Razzetti, E., Vamberger, M., Vences, M., Vörös, J., & Crochet, P.-A. (2020). Species list of the European herpetofauna

- 2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. *Amphibia-Reptilia*, 41, 139–189.
- Stapanian, M. A., Micacchion, M., & Adams, J. V. (2015). Wetland habitat disturbance best predicts metrics of an amphibian index of biotic integrity. *Ecological Indicators*, 56, 237–242.
- Suggitt, A. J., Fey, S. B., Vasseur, D. A., Alujević, K., Kroeker, K. J., Logan, M. L., O'Connor, M. I., Rudolf, V. H. W., DeLong, J. P., Peacor, S., Selden, R. L., Sih, A., & Clusella-Trullas, S. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, 8, 713–717.
- Sykora-Bodie, S. T., Álvarez-Romero, J. G., Adams, V. M., Gurney, G. G., Cleary, J., Pressey, R. L., & Ban, N. C. (2021). Methods for identifying spatially referenced conservation needs and opportunities. *Biological Conservation*, 260, 109138.
- Taylor, R. G., Scanlon, B., Döll, P., Rodell, M., Van Beek, R., Wada, Y., Longuevergne, L., Leblanc, M., Famiglietti, J. S., Edmunds, M., Konikow, L., Green, T. R., Chen, J., Taniguchi, M., Bierkens, M. F. P., MacDonald, A., Fan, Y., Maxwell, R. M., Yechieli, Y., & Treidel, H. (2013). Ground water and climate change. *Nature Climate Change*, 3, 322–329.
- Viceto, C., Cardoso Pereira, S., & Rocha, A. (2019). Climate change projections of extreme temperatures for the Iberian Peninsula. *Atmosphere*, 10, 229.
- Weeks, A. R., Sgro, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, K. A., Byrne, M., Coates, D. J., Eldridge, M. D., Sunnucks, P., Breed, M. F., James, E. A., & Hoffmann, A. A. (2011). Assessing the benefits and risks of translocations in changing environments: A genetic perspective. *Evolutionary Applications*, 4, 709–725.
- Wiedenfeld, D. A., Alberts, A. C., Angulo, A., Bennett, E. L., Byers, O., Contreras-MacBeath, T., Drummond, G., da Fonseca, G. A. B., Gascon, C., Harrison, I., Heard, N., Hochkirch, A., Konstant, W., Langhammer, P. F., Langrand, O., Launay, F., Lebbin, D. J., Lieberman, S., Long, B., & Zhang, L. (2021). Conservation resource allocation, small population resiliency, and the fallacy of conservation triage. *Conservation Biology*, 35, 1388–1395.
- Williams, J. W., ST, J., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, 104, 5738–5742.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Alagador, D. (2022). Effective conservation planning of Iberian amphibians based on a regionalization of climate-driven range shifts. *Conservation Biology*, e14026. <https://doi.org/10.1111/cobi.14026>