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Climate Change Effects on the Only Western Palearctic Plethodontids: Range Changes and Possible Depletion of Intraspecific Genetic Diversity

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ABSTRACT

Aim: Amphibians are particularly sensitive to rapid climatic shifts, due to their eco-physiology, life history traits and high frequency of narrowly distributed species. The genus *Speleomantes* encompasses the only extant Western Palearctic plethodontids, with three species occurring in peninsular Italy and the remaining five endemic to Sardinia Island.

Given the restricted ranges of *Speleomantes* species and their vulnerability to environmental change, we implemented Ecological Niche Models (ENMs) to estimate the likely impacts of various global warming scenarios on the extent and geographical location of climatically suitable areas.

Time Period: Current, with ENMs projected to 2030, 2050 and 2070 under alternative Shared Socioeconomic Pathways.

Location: Italian Peninsula and Sardinia Island.

Major Taxa Studied: *Speleomantes* Dubois 1984 (Caudata: Plethodontidae).

Methods: Ensembles of ENMs were fitted for each *Speleomantes* species, using the 'biomod2' modelling platform in R environment. Then, post-modelling analyses were applied in GIS environment to highlight: (i) the primary geographic direction of predicted suitability shifts for each species and (ii) the proportion of stable, gained and lost suitable areas for each genetic lineage of the single species.

Results: We found a noticeable shrinking of suitable areas for all *Speleomantes* species, being particularly extensive under 'business-as-usual' scenarios for the Sardinian ones. Moreover, core suitable areas were predicted to shift for most species and suitability losses emerged to differently affect distinct genetic lineages, posing additional challenges for designing effective conservation measures.

Main Conclusions: The predicted shrinkage and shifting of climatically suitable areas for most *Speleomantes* species point to the urgency of evaluating in due time alternative conservation strategies for these endemic urodeles, to prevent losses of taxonomic and genetic diversity. Our modelling framework may be applied to other species with similar traits (e.g., low dispersal ability and narrow environmental niche breadth) to predict climate-induced range contractions or shifts, using the gained information to optimise conservation outcomes.

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1 | Introduction

In the last few decades, amphibians underwent a dramatic decline that brought about half of the known species worldwide at risk of extinction, making them the most endangered group of vertebrates (Stuart et al. 2004; Beebe and Griffiths 2005; Luedtke et al. 2023). Amphibians are ectothermic organisms characterised by strict physiological requirements, frequently with limited dispersal abilities (Pough et al. 2016). These characteristics make amphibians particularly sensitive to multiple threats, spanning from habitat alteration to the introduction of alien species and infectious diseases, which can act synergistically and increase their detrimental effects (Collins and Storer 2003; Brook, Sodhi, and Bradshaw 2008; Martel et al. 2012; Grant et al. 2016). One of the main drivers of the amphibian crisis is climate change, as amphibians generally rely on external environmental conditions to regulate their body temperature and to maintain their skin, often involved in gas exchanges, moist (Pough et al. 2016; Blaustein et al. 2010). Higher temperatures and longer dry periods reduce availability of suitable habitats for amphibians, disrupting their phenology and breeding activity, also decreasing their fitness and survival (Ficetola and Maiorano 2016; Lunghi et al. 2018; Araújo, Thuiller, and Pearson 2006).

Plethodontid salamanders (Plethodontidae), with more than 500 species described, constitute the most abundant family of Urodela (AmphibiaWeb 2024). The biogeography of plethodontid salamanders is still debated: they are mainly distributed in the Americas, while eight species occur in Europe and only one in Asia (Min et al. 2005; Carranza et al. 2008; Shen et al. 2016). European cave salamanders (genus *Speleomantes*; sometimes referred as European *Hydromantes*, see Wake 2013 for further taxonomic discussion) are a group of allopatric species endemic (or sub-endemic) to Italy (Lanza et al. 2006). Three species (*S. strinatii* (Allen 1958), *S. ambrosii* (Lanza 1955), *S. italicus* (Dunn 1923)) occur in peninsular Italy, within the Maritime Alps and throughout the Apennine chain; only *S. strinatii* range stretches up to the French Provence. The other five species (*S. flavus* (Stefani 1969), *S. supramontis* (Lanza, Nascetti and Bullini 1986), *S. imperialis* (Stefani 1969), *S. sarrabusensis* (Lanza et al. 2001), *S. genei* (Temminck and Schlegel 1838)) are endemic to Sardinia island (Italy), where their distribution is mainly shaped by the local geomorphology (Chiari et al. 2012). The only known exceptions to such allopatric patterns are two small contact zones between mainland species, where viable hybrids occur (Ficetola et al. 2019; Bruni et al. 2023). A few introductions of these species outside their native range are also known (Lucente et al. 2016; Ginal et al. 2021; Schulz et al. 2021; Lunghi, Manenti, and Cimmaruta 2022).

Speleomantes are fully terrestrial salamanders characterised by the absence of lungs: gas exchange (i.e., breathing) mostly occurs through their skin, which must be constantly wet to guarantee its efficiency (Spotila 1972). These species therefore need specific microclimatic conditions to survive, including relatively low temperatures and high humidity (Lanza et al. 2006; Ficetola et al. 2018). Such conditions occur in surface environments mostly during autumn and spring but can be found in subterranean environments all year round (Lunghi, Manenti, and Ficetola 2015; Culver and Pipan 2019). Indeed, *Speleomantes*

individuals often exploit both natural and artificial subterranean environments where suitable microclimate occurs (Lunghi et al. 2018, 2022).

Despite the possibility of exploiting subterranean shelters, climate change remains one of the main threats to *Speleomantes* (Rondinini, Battistoni, and Teofili 2022). First, external climate is intimately connected with the inner microclimatic conditions of subterranean environments, where it mostly affects the areas close to the entrance (Badino 2004; Lunghi, Manenti, and Ficetola 2015; Culver and Pipan 2019). Thus, the increase of temperature and dryness at the surface caused by global warming will also be replicated in the shallowest areas of subterranean environments (Mammola et al. 2019), reducing the availability of suitable habitats and therefore representing a threat to many cave-dwelling species (Rizzo et al. 2015; Sánchez-Fernández et al. 2016; Mammola, Goodacre, and Isaia 2018). Secondly, as facultative cave-dwellers (so-called troglophiles; Howarth and Moldovan 2018), *Speleomantes* often forage on the surface, where prey is more abundant (Lunghi et al. 2018; Culver and Pipan 2019). Climate change may reduce prey availability in both surface and subterranean habitats, confining salamanders to deep, resource-poor spaces (Salvidio et al. 1994; Lunghi et al. 2018).

Given these multiple climate change-related threats on *Speleomantes*, we aim to assess potential shifts in the extent of suitable areas for the eight *Speleomantes* species under multiple emission scenarios up to 50 years in the future, using state-of-the-art climatic projections and ecological niche modelling techniques. *Speleomantes* are a group of highly threatened species (1 NT, 1 VU, 4 EN, 2 CR; www.iucnredlist.org, accessed on 19/05/2023) not only because of the specific microclimatic conditions required for their survival (Spotila 1972) but also because of their high longevity (up to 25 years) and long generation time (2 years to complete a reproductive cycle) (Lunghi et al. 2018; Lunghi 2022). A period of 50 years (the timespan of our models' predictions) corresponds to approximately two generations for *Speleomantes* (Lunghi 2022); thus, our predictions correspond to a time horizon for which it is improbable that these salamanders will develop adaptive traits fast enough to mitigate climate change impacts (Bürger and Lynch 1995; Visser 2008).

We first create a suitability map for each of the eight *Speleomantes* species by correlating occurrence data from their current range to climatic conditions within an ensemble modelling framework, and we then predict how suitability would change according to the different climatic projections considered. Specifically, we estimate: (i) the variation of (climatic) habitat suitability at each known current occurrence site and (ii) whether and how the suitable area for each species will change, both in extent and in its geographic occurrence.

We finally combine our predictive models with available genetic data for all the species, to infer how suitability variations might impact haplotype diversity, through an original approach coupling post-modelling GIS-based analyses with spatially referred genetic data. This point is important because even a similar overall magnitude of climate change-induced habitat loss can affect species differently based on the spatial distribution of genetic diversity (e.g., Pauls et al. 2013; Abreu-Jardim et al. 2021).

While some species can be uniformly affected by suitability losses across their haplotypes' network, others could experience more patchy impacts (Wróblewska and Mirski 2018; Abreu-Jardim et al. 2021). If certain haplotypes are disproportionately affected, compared to others, in terms of spatial overlap with the areas where suitability loss is inferred, this could lead to genetic impoverishment.

Identifying this phenomenon is thus crucial to support spatial prioritisation in conservation plans. While our study centres on *Speleomantes*, the framework we present is broadly adaptable to other taxa and cases facing similar climate-related pressures. By integrating climate modelling with genetic data, this approach offers a valuable tool to understand and mitigate the effects of habitat shifts on biodiversity, suited to species with peculiar genetic distributions and habitat needs (e.g., Abreu-Jardim et al. 2021). To assist researchers in evaluating its broader applicability, we provide an overview of the framework in Figure 1, which summarises the key steps and considerations, enabling others to quickly assess its relevance to their study cases and explore potential applications.

2 | Materials and Methods

2.1 | Data Description

The occurrence localities dataset was created by integrating data from bibliographical sources, museum records and fieldwork spanning from 1969 to 2017, and validated through the most recent research on *Speleomantes* (Ficetola et al. 2018). A further validation was performed by comparing the gathered data with the IUCN Red List range maps (IUCN SSC Amphibian Specialist Group 2022a, 2022b, 2022c, 2022d, 2022e, 2022f,

2022g, 2022h). Data were then filtered to remove duplicates and erroneous records.

Considering that special care should be taken in publishing information about occurrence localities of these sensitive amphibians due to the risk of data exploitation by poachers (Lunghi et al. 2019), the occurrence records used for our analyses are provided in Table S1a but their geographic coordinates (WGS 84—EPSG 4326) are rounded to 0.01° (~1.1 km).

2.2 | Model Building

Nineteen bioclimatic variables for both current and future scenarios (2030, 2050 and 2070) (resolution: 30 arc-seconds, ~1 km) were downloaded from the Worldclim repository (version 2.1) (Fick and Hijmans 2017) and used as candidate predictors (detailed information about these variables is provided in Table S1b). We selected all the four CMIP6 Shared Socio-economic Pathways (SSPs, narratives considering both climate change and social and economic projections) available, namely the SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, to encompass all the different scenarios which the target species may face in the future (Riahi et al. 2017). As future suitability predictions may vary depending on the specific General Circulation Models (GCMs) used to project the ENMs (Stralberg et al. 2015), we mitigated this issue by using three different GCMs, the BCC-CSM2-MR (Wu et al. 2019), the IPSL-CM6ALR (Boucher et al. 2020) and MIROC6 (Tatebe et al. 2019) and then averaging the corresponding outputs (see Section 2.3). To test for possible multi-collinearity among the predictors, the 'Variance Inflation Factor' (VIF) (Dormann et al. 2013; Guisan, Thuiller, and Zimmermann 2017) was computed in the R environment (R Core Team 2022) using the

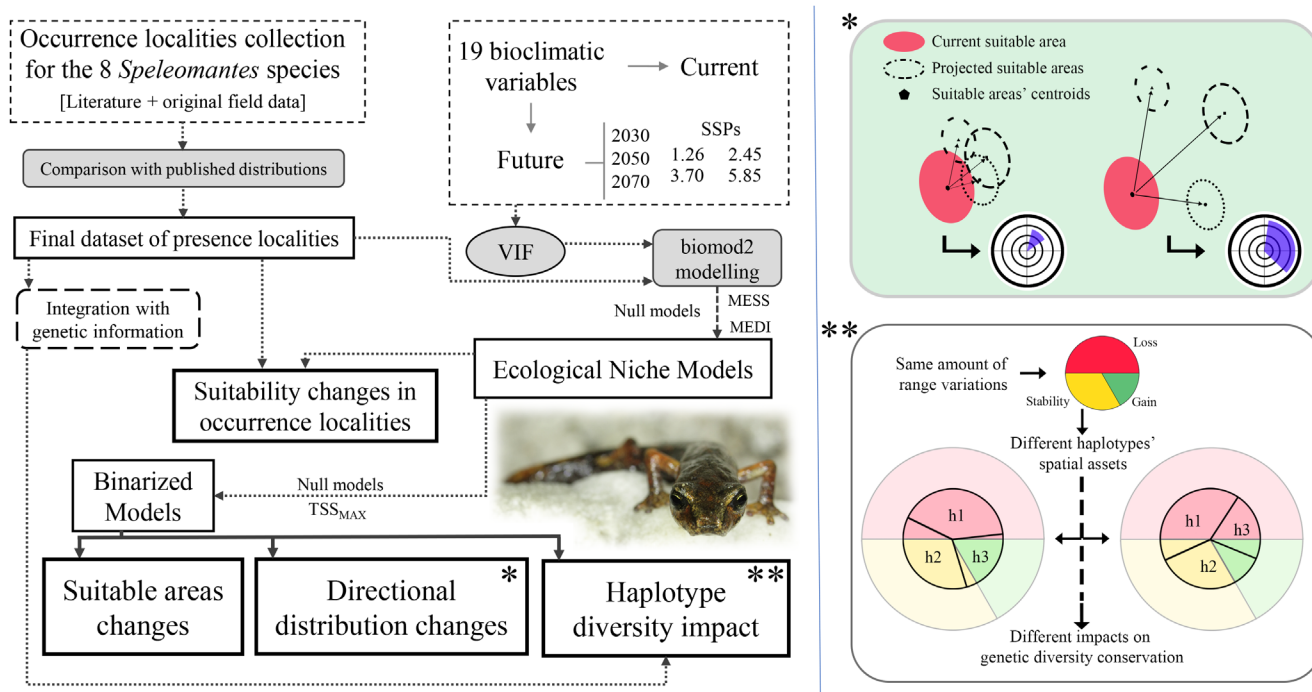


FIGURE 1 | Overall analytical framework (left) and rationale of the analyses focusing on distribution changes (*) and haplotype diversity impact (**).

'vifstep' function implemented in the 'usdm' package (Naimi et al. 2014). This function computes the predictors' VIF by iteratively regressing one predictor against the others, finally excluding those predictors exceeding the user-defined threshold. Here, the threshold was set at $VIF \geq 10$, following Guisan, Thuiller, and Zimmermann (2017). Current knowledge about the ecology and physiology of the target species was considered when selecting the final set of predictors after the VIF analysis (Brandt et al. 2017). To avoid model overfit, possible clusters of occurrence data were rarefied by thinning them at the working spatial resolution (Sillero and Barbosa 2021; Sillero et al. 2021); these datasets were used to forecast the species realised niche (*sensu* Sillero 2011) by using correlative Ecological Niche Models (ENMs) and standard procedures (Sillero et al. 2021).

The ENMs were built using the 'biomod2' R package, and their predictions were later combined to obtain the Ensemble Models (Araújo and New 2007). To encompass regression-based, hybrid and machine learning modelling approaches, the following algorithms were chosen in the 'BIOMOD_Modelling' function: Generalised Linear Models (GLMs), Gradient Boosting Models (GBM, commonly known as Boosted Regression Trees—BRT) and Random Forest (RF), at their default values.

2.3 | Model Validation and Ensemble Modelling

Ten sets of 1000 pseudo-absences were generated through the Surface Range Envelope (SRE) algorithm (PA.strategy='sre' and PA.sre.quant=0.05 within the 'BIOMOD_FormatingData' function), so that pseudo-absences were generated by omitting any pixel hosting climatic conditions comprised within the 95th percentile of the distribution of values observed for presence locations (Barbet-Massin et al. 2012). For each algorithm and set of pseudo-absences, 10 model fitting iterations were performed, with 80% of the initial dataset used to build the models and the remaining 20% used for validation. A total of 80 models (8 species \times 10 replicates) were obtained, leading to 2880 individual model projections (8 species \times 10 replicates \times 3 future years \times 4 SSPs \times 3 GCMs).

The area under the curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Phillips, Anderson, and Schapire 2006) and the True Skill Statistic (TSS) (Allouche, Tsoar, and Kadmon 2006) were calculated for each individual model. Further, to test whether the calibration performance of the ENMs was significantly better than random, null models were fitted for each target species following Raes and ter Steege (2007). For each species, 1000 sets of pseudo-presence points randomly distributed across the study area were generated with a Poisson distribution and the same number of records as the empirical presences. Additionally, a set of pseudo-absences equalling the actual *Speleomantes* species' occurrences were randomly drawn within unsuitable areas defined through the same SRE algorithm described above. We ran the models with the same algorithms and parameters as the empirical models and calculated the evaluation metrics. We compared the empirical and null evaluation metrics with a Wilcoxon test for paired records. Then, the obtained null distribution of AUC and TSS values averaged across the three algorithms, were compared to

the scores obtained by the ENMs fitted on the real occurrences of the target species: empirical ENMs with AUC and TSS scores higher than the 95th percentile of the obtained null distribution were selected to enter the Ensemble Modelling process.

The Ensemble Models were calculated with the 'BIOMOD_EnsembleModeling' function (Thuiller, Georges, and Engler 2023), obtaining both the weighted average of probabilities (*wmean*) and their coefficient of variation (*cv*). Current ENMs were projected to the three different future climate scenarios (SSP narratives 1.26, 2.45, 3.70 and 5.85) for each year (2030, 2050 and 2070).

Then, to deal with the uncertainty in future predictions, we computed the Multivariate Environmental Similarity Surface (MESS) (Elith and Leathwick 2009) through the homonymous function from the 'dismo' R package (Hijmans and Elith 2016). The resulting MESS maps were subsequently used as input to derive the Multivariate Environmental Dissimilarity Index (MEDI), following the formula by Iannella, Cerasoli, and Biondi (2017). This index calculates a weighted average for the ENM projections from different GCMs based on their corresponding MEDI values (Iannella, Cerasoli, and Biondi 2017). The weighted predictions obtained based on the MEDI were then binarized using the max TSS threshold (Liu, White, and Newell 2013), to later perform the distribution changes' analyses. The 'ecospat.max.tss' function from the 'ecospat' R package (Di Cola et al. 2017) was applied to calculate the suitability value maximising the TSS, and thus used as binarization threshold.

2.4 | Post-Modelling Analyses

As *Speleomantes* have a high site fidelity and low dispersal ability (Lanza et al. 2006; Salvidio 2013; Lunghi and Bruni 2018), we only considered a scenario of null dispersal for interpreting our results (Carvalho et al. 2010). This means that any suitable habitat outside the current distribution range will not be reached by the species. Binarized maps were implemented in the 'Distribution changes between binary SDMs' algorithm of the SDMtoolbox in ArcGIS Pro. This tool permits us to obtain the direction and magnitude of the shift that the centroids of the binarized model predictions are expected to undergo over the years. The obtained outputs (corresponding to each combination of species \times year \times SSP) were summarised into compass charts, where the width of a sector represents the mean and standard deviation of the shift's direction, while the distance from the chart centre represents the magnitude of the shift (Rationale in Figure 1).

Moreover, the binary maps were processed through the 'BIOMOD_RangeSize' function implemented in the 'biomod2' package. This function calculates the suitable areas that are expected to be gained, kept or lost for each considered future scenario, comparing the current and future binarized predictions.

We then coupled the resulting outputs with the ones obtained from the 'Split binary SDM by input clade relationship' tool of the SDMtoolbox, which divides binarized predictions based on a haplotype network of the target species. For this aim, we collected haplotype data (Aruggi 2007; Chiari et al. 2012;

Cimmaruta, Lucente, and Nascetti 2015) for the eight species considered. Specifically, we chose to deepen the assessment of possible changes in suitable areas at an intraspecific level of diversity because this is expected to provide more comprehensive management information than the quantification of potential suitability shifts at the species level alone (Iannella, D'Alessandro, and Biondi 2018; Maia-Carvalho et al. 2018; Cerasoli et al. 2021). In fact, if a currently suitable area is predicted to be lost, the impact on conservation needs will vary depending on the spatial distribution of genetic diversity across populations. Habitat changes may affect a lineage entirely or in part, influencing the kind of conservation actions required to preserve genetic diversity, with some areas being more critical due to unique genetic compositions (Figure 1).

3 | Results

The occurrence database (max spatial uncertainty = 100 m) generated for the eight *Speleomantes* species consisted of 883 records obtained from literature and field data, out of which 142 belonged to *Speleomantes strinatii*, 197 to *S. ambrosii*, 298 to *S. italicus*, 41 to *S. flavus*, 62 to *S. genei*, 80 to *S. imperialis*, 16 to *S. sarrabusensis* and 47 to *S. supramontis*. After filtering data (exclusion of duplicate and erroneous records), the remaining 620 presence localities were distributed as follows: 115 for *S. strinatii*, 77 for *S. ambrosii*, 262 for *S. italicus*, 26 for *S. flavus*, 46 for *S. genei*, 53 for *S. imperialis*, 12 for *S. sarrabusensis* and 28 for *S. supramontis*. To summarise this information, the minimum convex polygons built over the occurrence localities of each species are shown in Figure 2a.

We selected eight bioclimatic variables (BIO01, BIO07, BIO08, BIO11, BIO12, BIO15, BIO16 and BIO19) as predictors (VIF < 10). Models' discrimination capability was high for all the species, according to the obtained AUC and TSS values (AUC_{strinatii} = 0.965, TSS_{strinatii} = 0.898; AUC_{ambrosii} = 0.954, TSS_{ambrosii} = 0.899; AUC_{italicus} = 0.977, TSS_{italicus} = 0.897; AUC_{imperialis} = 0.882, TSS_{imperialis} = 0.720; AUC_{genei} = 0.930, TSS_{genei} = 0.828; AUC_{supramontis} = 0.938, TSS_{supramontis} = 0.862; AUC_{flavus} = 0.957, TSS_{flavus} = 0.899; AUC_{sarrabusensis} = 0.944, TSS_{sarrabusensis} = 0.902). These values were also higher than 95% of those from the corresponding null distribution, confirming that the obtained ENM performed significantly better than null models (Figure S1). Within the calibrated ENMs, the most contributing variables for all *Speleomantes* species were those related to precipitation. Specifically, precipitation seasonality (BIO15) emerged as one of the most important variables, followed by the precipitation in the wettest quarter (BIO16) and annual precipitation (BIO12).

Habitat suitability maps resulting from the models calibrated on current climatic conditions (Figure 2b–i) showed a spatial arrangement of predicted suitable areas generally coincident with the species' known distribution. In fact, the highest suitability for each species overlapped with its known distribution, covering most of the respective minimum convex polygon (Figure 2b–d). Aside from some high suitability patches being far from the species' current range, it also appeared that medium suitability areas extend further from the 'core' distribution for all the species.

For the peninsular *Speleomantes* species, a slight decrease in suitability throughout the whole calibration area is expected in all the considered future scenarios (Figure 3a; MEDI-corrected models for each timeframe-SSP considered are reported in Figure S2). Further, the decrease in suitability was progressively higher when moving towards the more distant future and from the best to the worst SSP scenario (i.e., SSP1-2.6 to SSP5-8.5). When considering the Sardinian species, the reduction of suitable area was more extensive, especially for the three species with narrower distribution (i.e., *S. flavus*, *S. sarrabusensis*, and *S. supramontis*; Figure 3a, Figure S2).

When focusing on the current occurrence localities, the same trends inferred at the study area scale emerged: an average of the considered time frames (i.e., the average of projections for 2030, 2050 and 2070, calculated to streamline figure presentation and ensure brevity; full data available in Table S2) indicated a higher magnitude of suitability loss for the Sardinian species compared to the peninsular ones (Figure 3b, Figure S2). As for the peninsular species, a predominance of the high suitability classes emerged for *S. strinatii* and *S. ambrosii* in all the SSPs considered, while for *S. italicus* the suitability classes were evenly distributed (Figure 3c–f, Figure S2). Considering the Sardinian species, the suitability over current occurrence localities dropped in all SSP scenarios for *S. flavus*, *S. sarrabusensis*, and *S. supramontis* (Figure 3c–f, Figure S2), as already observed for the suitability predicted at the study area scale (Figure 3a), with the highest percentage of occurrences falling into low-suitability classes (Figure 3c–f, Figure S2). On the other hand, some *S. genei* and *S. imperialis* occurrences were predicted to fall into highly suitable areas, even though the suitability deteriorating trend from recent-to-far future and SSP-1.26-to-SSP5-8.5 scenarios is still visible for both (Figure 3c–f, Figure S2).

The future suitability changes also produced some shifts in the binarized suitable areas inferred for each species under current conditions. In the averaged binarized future scenarios (i.e., the average among 2030, 2050 and 2070 projections, computed for brevity and to avoid overcrowding the figures; results in full are available in Table S3), the areas suitable for *S. strinatii* shifted northwards, with a more pronounced shift in the SSP5-8.5 which is also accompanied by notable variability (i.e., a wider compass) among the three projection years (Figure 4, upper row). The shifts of *S. ambrosii* were instead predicted to be much smaller and pointing towards the northeast (Figure 4, upper row); for *S. italicus*, a westward shift was observed, except for the SSP3-7.0, where a north-eastern change was predicted (Figure 4, upper row).

Comparing the shifts of the binarized suitable areas predicted for the Sardinian species with those of the peninsular ones, two main trends emerged: the magnitude of the shifts was much smaller for the Sardinian species, except for *S. genei* and variability in the averaged future predictions (i.e., the predicted shifts point towards the same direction throughout the years) was low as well. Specifically, suitable areas for *S. genei* and *S. imperialis* were predicted to shift towards the northeast, in all the SSP scenarios, with greater extents compared to the other three Sardinian species (Figure 4, lower row). Also, the predicted shifts of *S. flavus* and *S. supramontis* appeared rather stable throughout the SSP scenarios, heading south and southeast,

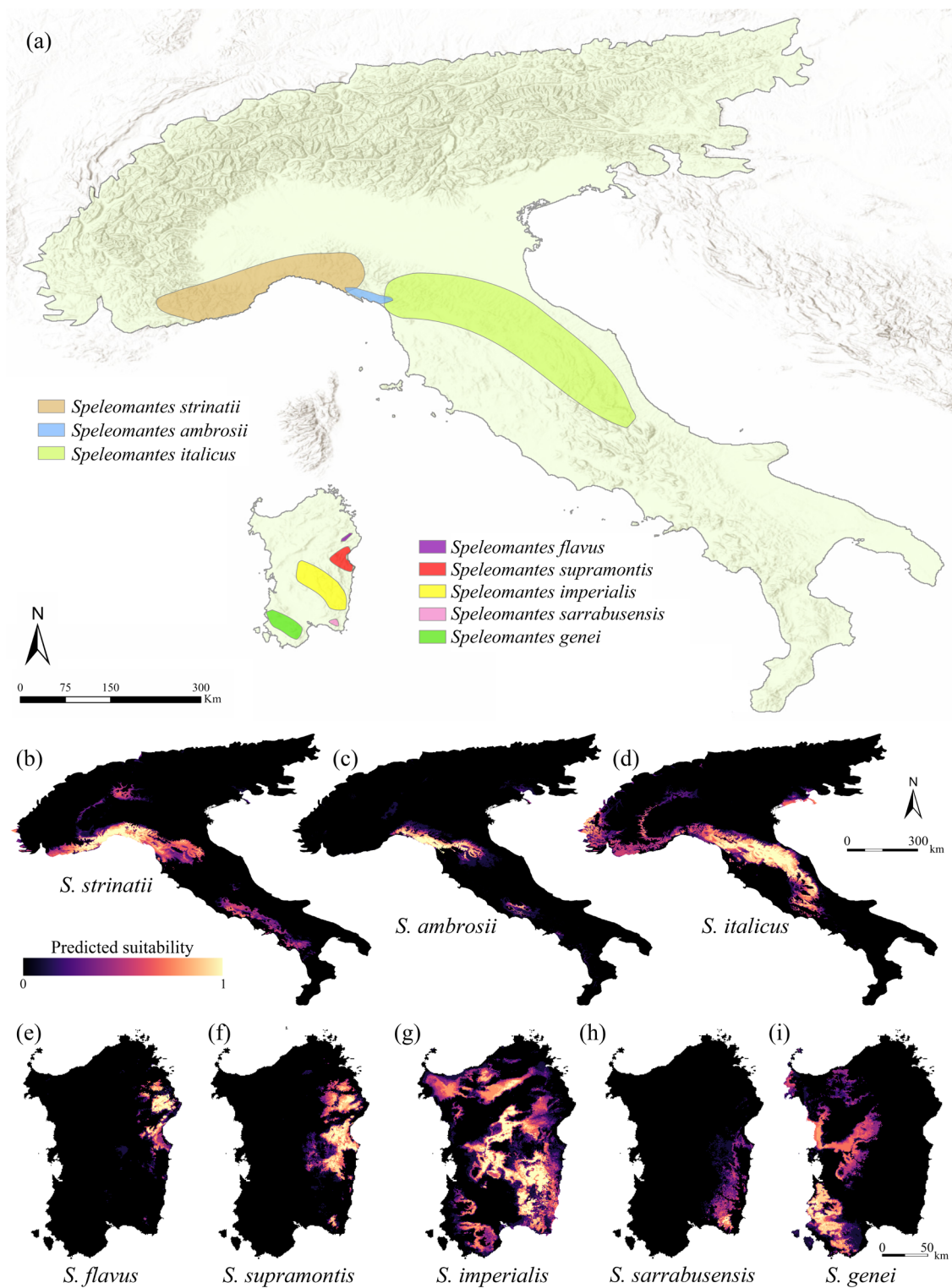


FIGURE 2 | (a) Current distribution of the eight *Speleomantes* species; (b–i) predicted habitat suitability for each *Speleomantes* species for the current climatic conditions.

respectively (Figure 4, lower). The only exception to such stability in the direction of the suitability shifts was found for *S. sarrabusensis*, whose predicted shifts' direction heavily depended upon the SSP considered (Figure 4, lower).

When applying the predicted future suitability changes (in terms of gain, stability and loss of suitable territories) to the haplotype

diversity of the eight *Speleomantes* species, a twin-track pattern emerged for peninsular and Sardinian species (Figure 5, Table S4). In fact, while the peninsular species showed a higher haplotype diversity combined with a predominance of future stability in currently suitable areas (Figure 5, upper), the Sardinian ones showed lower haplotype diversity and much higher loss of suitable territories (Figure 5, lower). Moreover, some Sardinian

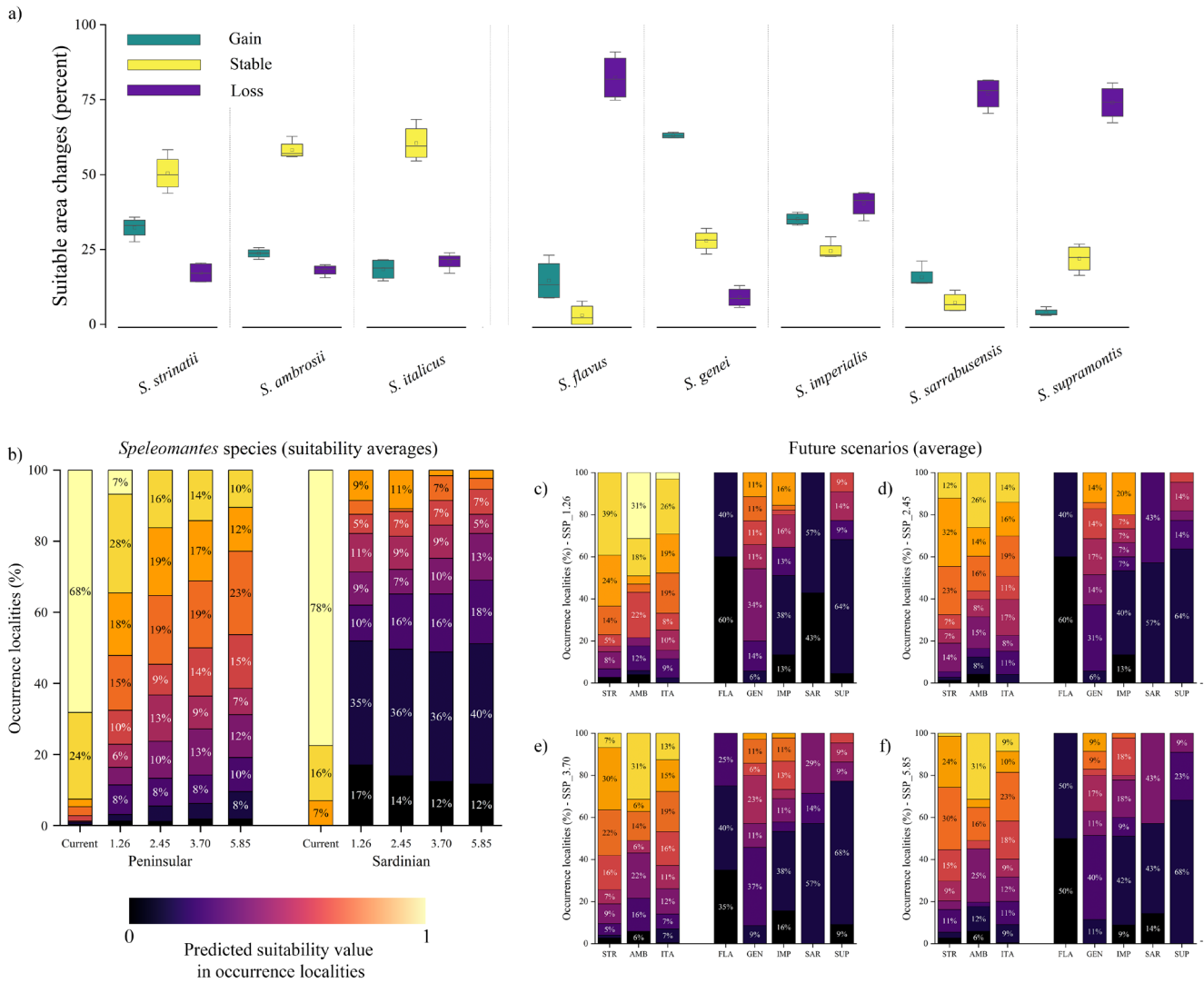


FIGURE 3 | (a) Changes in the binarized predicted suitable areas for each *Speleomantes* species, resulting from the average of the 2030, 2050 and 2070 future predictions, and all the four SSP scenarios considered; (b) Predicted suitability extracted in occurrence localities as an average among Peninsular and Sardinian species, for current and future predictions; (c–f) Predicted averaged suitability (all future predictions), for each SSP considered, extracted in each species' occurrence locality; AMB, *S. ambrosii*; FLA, *S. flavus*; GEN, *S. genei*; IMP, *S. imperialis*; ITA, *S. italicus*; SAR, *S. sarrabusensis*; STR, *Speleomantes strinatii*; SUP, *S. supramontis*.

species showing few haplotypes were also predicted to lose most of the corresponding suitable territories. This is particularly concerning for those species/haplotype combinations occurring in small ranges (e.g., the h1 and h2 groups of *S. flavus* and *S. sarrabusensis*) (Figure 5, lower).

4 | Discussion

Climate change represents one of the major threats affecting biodiversity on a global scale (Bellard et al. 2012). Its effects are particularly intense for microendemic species, especially for those that completely rely on the environment for their thermoregulation (Spotila 1972; Lunghi et al. 2016). Using four different predictive scenarios spanning up to 50 years in the future, we identified important, negative effects that climate change may have on eight amphibian species belonging to the genus *Speleomantes*, the only representatives of the family Plethodontidae in Europe (Lanza et al. 2006). Climatic

suitability is predicted to decrease for all *Speleomantes* species, leading to unsuitable conditions in most of the historical occurrence sites (Figure 3b). Sardinian *Speleomantes* are the most affected species, with a high probability of climatic conditions becoming highly unsuitable in at least 50% of the current sites, compromising the species' persistence. For example, on average, for *S. supramontis* and *S. sarrabusensis* the climatic suitability for >80% of their occurrence sites will drop to less than 0.3 (in a 0-to-1 scale); this percentage reaches 100% for *S. flavus*, with about 94% of current occurrences showing a decrease in suitability below 0.2. A study involving the latter species highlighted a significant reduction of fitness-related traits (e.g., body condition index, local abundance, population densities) in populations located at sites in which climatic suitability was in the range of 0.3–0.4, resulting in a drop of the estimated population density up to 30 folds compared to the sites with better conditions (Lunghi et al. 2018). Our predicted scenarios have important implications for *Speleomantes* conservation, as the very low climatic suitability may drive species extinctions at the

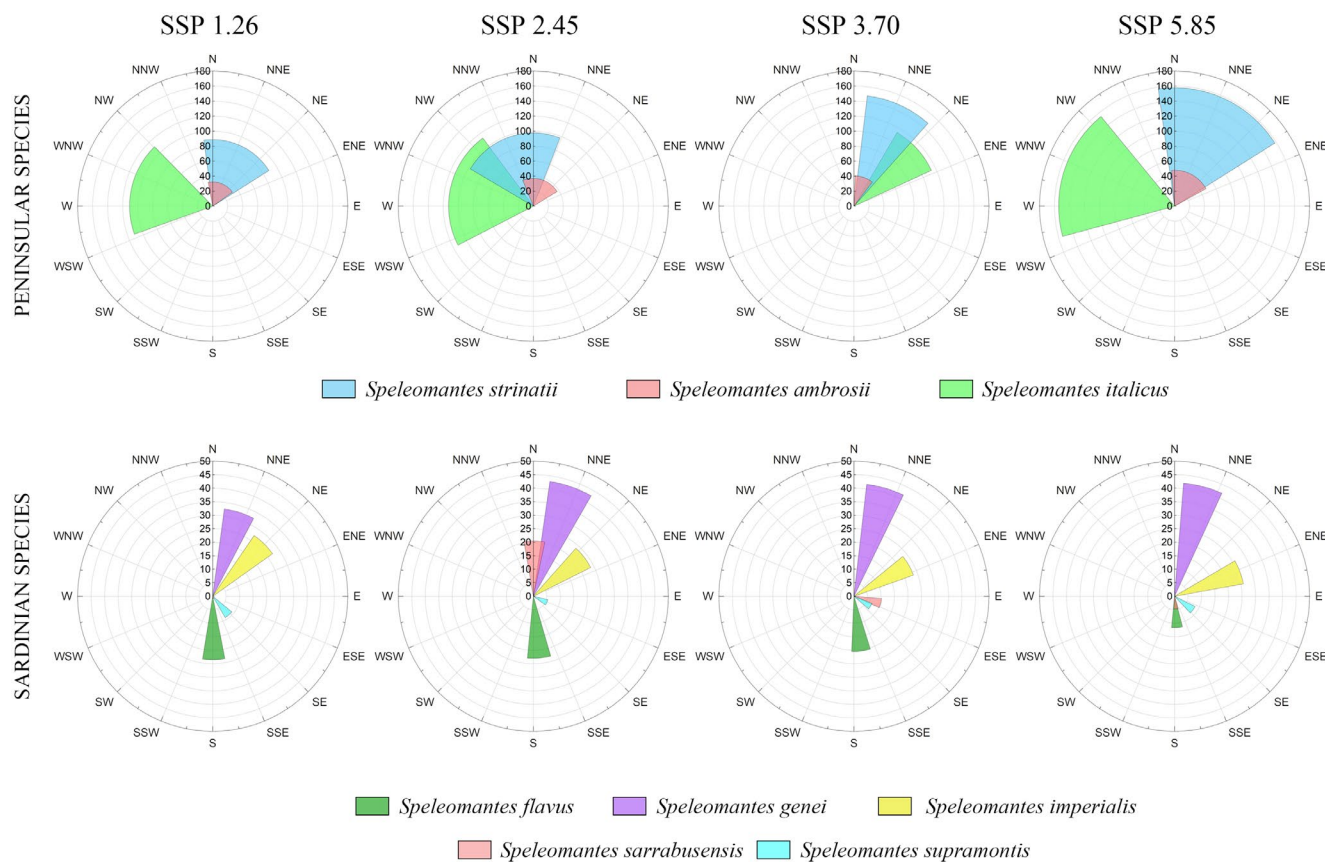


FIGURE 4 | Predicted shifts of suitable territories for the eight *Speleomantes* species under averaged future (2030, 2050, 2070) predictions for each SSP considered (circular sectors' width = coefficient of variation; radius = magnitude [in km] of the predicted shift).

local scale (Lowe 2011), provoking genetic erosion (Figure 5) and reducing the species' potential to persist and adapt to novel environmental conditions (Chown et al. 2010; Balart-García et al. 2023). A peculiar case is represented by *S. sarrabusensis*. This species has a range < 70 km² and is the only *Speleomantes* species that occurs in an area characterised by granitic rocks (Lanza et al. 2006; Carmignani et al. 2016); thus, it does not have subterranean climate change refugia as the other congeneric species, and it will cope worse with the upcoming global warming. A few artificial springs may serve as subterranean refugia for a specific population; nonetheless, a decline in the abundance of this population has been already detected over the past few years (Cogoni et al. 2023). Given the lacking access to caves due to the surrounding granitic terrain, any climate change-induced reduction in surface suitability will have a direct impact on this species, as it cannot retreat to subterranean habitats hosting more stable conditions (Salvidio et al. 1994; Lunghi et al. 2018).

Arenas-Castro and Sillero et al. (2021) also predicted a general decrease in the habitat suitability trends of *S. italicus* and *S. strinatii* over time based on ENMs calculated with a temporal series of satellite remote sensing products.

Based on our projections (Figure S2), all *Speleomantes* species will experience a strong loss of suitable area, an event that is particularly concerning for the long-term persistence of the Sardinian endemics (Figure 3). This is probably due to different potential causes which can act synergistically. *Speleomantes* show high site fidelity and low dispersal ability (Lanza

et al. 2006; Salvidio 2013; Lunghi and Bruni 2018), features that strongly reduce the populations' ability to avoid novel unsuitable environmental conditions (Bürger and Lynch 1995; Hill, Griffiths, and Thomas 2011; Pittman, Osbourn, and Semlitsch 2013). This is why we are considering a scenario of null dispersal for interpreting our results (Carvalho et al. 2010). Indeed, individuals probably will not disperse fast enough to reach new future suitable areas, thus remaining trapped in their subterranean refugia. Here, climate change will progressively confine them to the deepest oligotrophic areas where trophic supply is probably insufficient for the sustenance of the entire population (Lunghi et al. 2018; Culver and Pipan 2019; Mammola et al. 2019). Additionally, natural barriers may play an important role in limiting *Speleomantes* dispersal. Mainland *Speleomantes* species occur along the continuous mountainous area that spans from southern France to south-eastern Italy, including the Maritime Alps, Apuan Alps and the Apennine chain (Lanza et al. 2006). In this case, higher environmental connectivity (either above or below ground) may allow mainland *Speleomantes* to partially compensate for the loss of currently suitable areas by moving towards new ones (Figure 4). A completely different destiny is expected for insular species. Within Sardinia, the distribution of the five allopatric *Speleomantes* species is naturally shaped by the geomorphology of the island (Chiari et al. 2012), meaning that natural barriers are already preventing species from colonising new environments and co-occur. For example, *S. flavus* and *S. supramontis* are endemic to the nearby namesake massifs located in the northeastern part of the island (Lanza

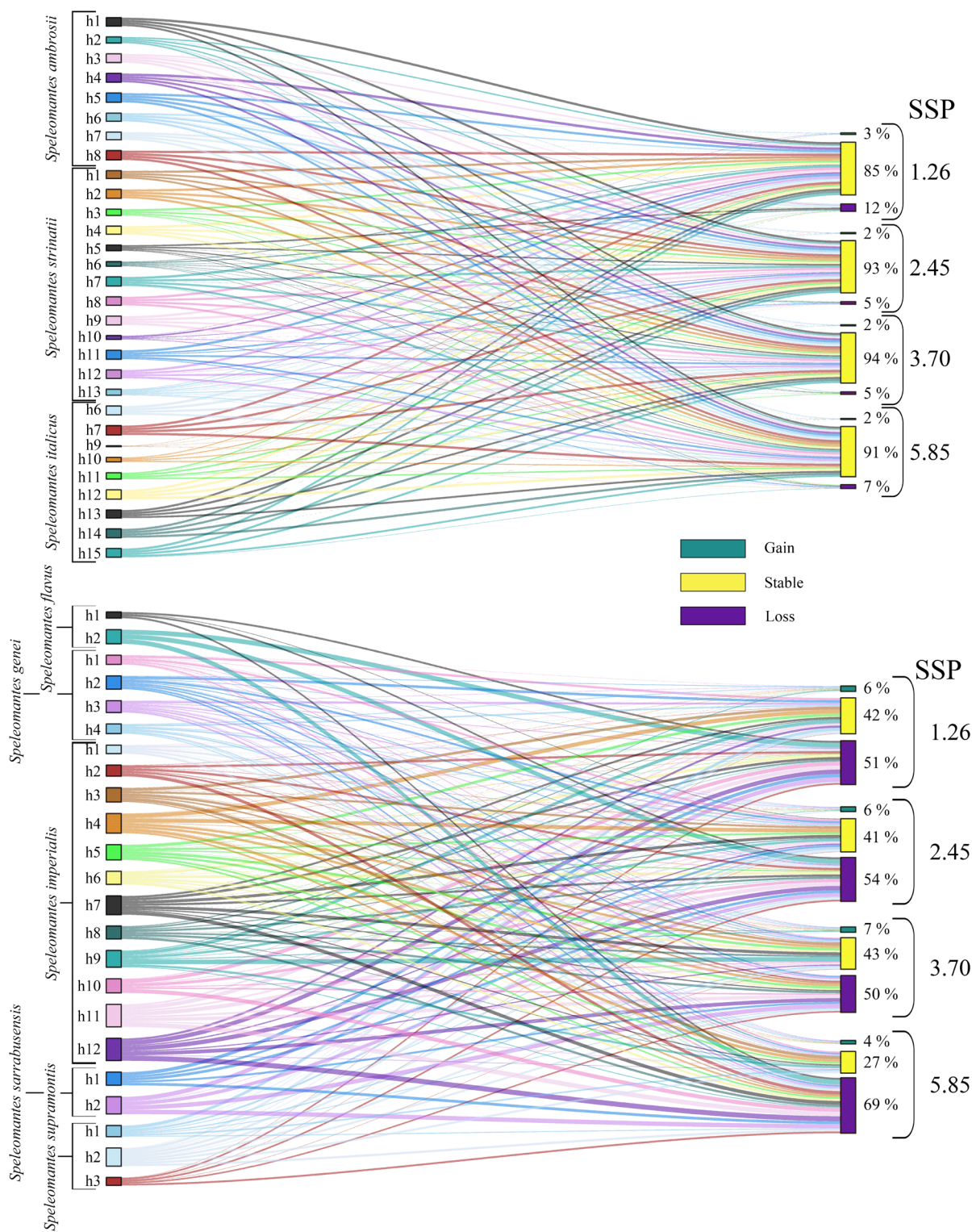


FIGURE 5 | Sankey charts for Peninsular (above) and Sardinian (below) *Speleomantes* species, reporting their respective haplotypes' future range changes (averages of 2030, 2050, 2070 scenarios) for the different SSPs considered.

et al. 2006). According to our predictions, the suitable climatic area for *S. supramontis* will shift towards the coast (Figure 4), where the species is naturally absent due to the lack of suitable habitats (i.e., lack of forests, high airborne salinity). On the other hand, the suitable climatic conditions for *S. flavus* are predicted to move southward, partially overlapping the actual distribution of *S. supramontis* (Figure 4). The two species are naturally isolated by the valley between the Monte Albo and

the Supramonte massif, a barrier that has been intensified by the construction of an arterial road (Lanza et al. 2006; Chiari et al. 2012). Both species, therefore, probably will not be able to track future shifts in the respective climatically suitable areas and colonise new localities, thus experiencing dramatic range losses. A further worsening is due to the unbalanced loss of species' genetic diversity. In fact, since a great directional loss of habitat suitability is predicted, the possibility of

geographically tracking changing conditions decreases in the patches located at the opposite sides of the shifts. This would be more detrimental for species with lower genetic diversity. When coupling this loss with the limited dispersal ability of *Speleomantes* (Lanza et al. 2006; Salvidio 2013; Lunghi and Bruni 2018) and their dependence upon environmental conditions (Lanza et al. 2006; Ficetola et al. 2018) which are possibly disrupted by climate change, a strategy of species- (or taxon-) specific assessment (Foden et al. 2013) and subsequent management (Pabijan et al. 2020) seems the only way to avoid local, when not complete, extinctions.

Our study highlights that climate change would represent a serious threat to the genus *Speleomantes* in the next few decades. In this short period, climatic conditions are predicted to become unsuitable in at least half of the current distribution for most of the eight species, trapping individuals into their subterranean climate change refugia and preventing the colonisation of new areas. The slow generation turnover that characterises these species is an additional factor hampering the chances of adapting to the novel environmental conditions. We therefore recall once again the attention to the urgency of reducing our impact on the climate, and more in general on natural environments, to avoid important biodiversity losses.

The highlighted threats to *Speleomantes* species align with broader trends observed among Mediterranean amphibians, as documented by Luedtke et al. (2023): amphibians in this area are particularly vulnerable due to the compounded impacts of climate change, habitat fragmentation and limited availability of refugia, with 41% of amphibian species globally now threatened with extinction. The Mediterranean region, already experiencing high biodiversity pressures, faces further risks of amphibian declines due to increasing aridification and temperature extremes, both of which reduce habitat suitability and survival rates for moisture-dependent species. Finally, we strongly promote the monitoring of *Speleomantes* populations to promptly buffer potential detrimental effects with appropriate conservation plans, also assessing the role of existing protected areas in safeguarding suitable territories for these species. Such efforts are essential not only for *Speleomantes* but also for preserving amphibian diversity across the Mediterranean, a hotspot of unique evolutionary lineages that are now highly imperilled.

Author Contributions

Mattia Iannella: conceptualization, formal analysis, investigation, original draft preparation, writing – review and editing, visualization. **Francesco Cerasoli:** formal analysis, investigation, original draft preparation, visualization, writing – review and editing. **Enrico Lunghi:** writing – review and editing. **Giulia Console:** data curation. **Maurizio Biondi:** data curation, original draft preparation. **Neftalí Sillero:** conceptualization, data curation, original draft preparation.

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Fieldwork data comprised only observational data on *Speleomantes* (no individuals handled or collected). No permits were required to gather such data.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Occurrence records of the target *Speleomantes* species, with geographic coordinates (WGS 84—EPSG 4326) rounded to 0.01° (~1.1 km, the same spatial resolution of the bioclimatic explanatory variables used to fit the Ecological Niche Models), are available as Supporting Information (Table S1). We also uploaded the occurrence records on the Dryad platform, where they are accessible at the following link: <https://doi.org/10.5061/dryad.np5hqc043>.

References

- Abreu-Jardim, T. P., L. Jardim, L. Ballesteros-Mejia, N. M. Maciel, and R. G. Collevatti. 2021. “Predicting Impacts of Global Climatic Change on Genetic and Phylogeographical Diversity of a Neotropical Treefrog.” *Diversity and Distributions* 27: 1519–1535.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. “Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS).” *Journal of Applied Ecology* 43: 1223–1232.
- AmphibiaWeb. 2024. Berkeley, CA: University of California. <https://amphibiaweb.org>. Last Accessed September 30th, 2024.
- Araújo, M. B., and M. New. 2007. “Ensemble Forecasting of Species Distributions.” *Trends in Ecology & Evolution* 22: 42–47.
- Araújo, M. B., W. Thuiller, and R. G. Pearson. 2006. “Climate Warming and the Decline of Amphibians and Reptiles in Europe.” *Journal of Biogeography* 33: 1712–1728.
- Arenas-Castro, S., and N. Sillero. 2021. “Cross-Scale Monitoring of Habitat Suitability Changes Using Satellite Time Series and Ecological Niche Models.” *Science of the Total Environment* 784: 147172. <https://doi.org/10.1016/j.scitotenv.2021.147172>.
- Aruggi, A. 2007. “Descrizione di una zona di contatto e ibridazione tra *Speleomantes italicus* e *Speleomantes ambrosii bianchii* (Amphibia—Plethodontidae) sulle Alpi Apuane mediante marcatori nucleari e mitocondriali.” Ph.D. thesis, University of Tuscia.
- Badino, G. 2004. “Cave Temperatures and Global Climatic Change.” *International Journal of Speleology* 33: 103–114.
- Balart-García, P., L. Aristide, T. M. Bradford, et al. 2023. “Parallel and Convergent Genomic Changes Underlie Independent Subterranean Colonization Across Beetles.” *Nature Communications* 14: 3842.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. “Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?” *Methods in Ecology and Evolution* 3: 327–338.
- Beebee, T. J. C., and R. A. Griffiths. 2005. “The Amphibian Decline Crisis: A Watershed for Conservation Biology?” *Biological Conservation* 125: 271–285.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. “Impacts of Climate Change on the Future of Biodiversity.” *Ecology Letters* 15: 365–377.
- Blaustein, A. R., S. C. Walls, B. A. Bancroft, J. J. Lawler, C. L. Searle, and S. S. Gervasi. 2010. “Direct and Indirect Effects of Climate Change on Amphibian Populations.” *Diversity* 2: 281–313.
- Boucher, O., J. Servonnat, A. L. Albright, et al. 2020. “Presentation and Evaluation of the IPSL-CM6A-LR Climate Model.” *Journal of Advances in Modeling Earth Systems* 12: e2019MS002010.
- Brandt, L. A., A. M. Benscoter, R. Harvey, et al. 2017. “Comparison of Climate Envelope Models Developed Using Expert-Selected Variables Versus Statistical Selection.” *Ecological Modelling* 345: 10–20.

- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. "Synergies Among Extinction Drivers Under Global Change." *Trends in Ecology & Evolution* 23: 453–460.
- Bürger, R., and M. Lynch. 1995. "Evolution and Extinction in a Changing Environment: A Quantitative-Genetic Analysis." *Evolution* 49: 151–163.
- Bruni, G., A. Chiochio, G. Nascetti, and R. Cimmaruta. 2023. "Different Patterns of Introgression in a Three Species Hybrid Zone Among European Cave Salamanders." *Ecology and Evolution* 13: e10437. <https://doi.org/10.1002/ece3.10437>.
- Carmignani, L., G. Oggiano, A. Funedda, P. Conti, and S. Pasci. 2016. "The Geological Map of Sardinia (Italy) at 1:250,000 Scale." *Journal of Maps* 12: 826–835.
- Carranza, S., A. Romano, E. N. Arnold, and G. Sotgiu. 2008. "Biogeography and Evolution of European Cave Salamanders, *Hydromantes* (Urodela: Plethodontidae), Inferred From mtDNA Sequences." *Journal of Biogeography* 35: 724–738.
- Carvalho, S. B., J. C. Brito, R. L. Pressey, E. Crespo, and H. P. Possingham. 2010. "Simulating the Effects of Using Different Types of Species Distribution Data in Reserve Selection." *Biological Conservation* 143: 426–438.
- Cerasoli, F., A. Besnard, M. Marchand, P. D'Alessandro, M. Iannella, and M. Biondi. 2021. "Determinants of Habitat Suitability Models Transferability Across Geographically Disjunct Populations: Insights From *Vipera ursinii ursinii*." *Ecology and Evolution* 11: 3991–4011.
- Chiari, Y., A. Meijden, M. Mucedda, J. M. Lourenço, A. Hochkirch, and M. Veith. 2012. "Phylogeography of Sardinian Cave Salamanders (Genus *Hydromantes*) Is Mainly Determined by Geomorphology." *PLoS One* 7: e32332.
- Chown, S. L., A. A. Hoffmann, T. N. Kristensen, M. J. J. Angilletta, N. C. Stenseth, and C. Pertoldi. 2010. "Adapting to Climate Change: A Perspective From Evolutionary Physiology." *Climate Research* 43: 3–15.
- Cimmaruta, R., D. Lucente, and G. Nascetti. 2015. "Persistence, Isolation and Diversification of a Naturally Fragmented Species in Local Refugia: The Case of *Hydromantes strinatii*." *PLoS One* 10: e0131298.
- Cogoni, R., M. Di Gregorio, F. Cianferoni, and E. Lunghi. 2023. "Monitoring of the Endangered Cave Salamander *Speleomantes sarra-busensis*." *Animals* 13: 391.
- Collins, J. P., and A. Storfer. 2003. "Global Amphibian Declines: Sorting the Hypotheses." *Diversity and Distributions* 9: 89–98.
- Culver, D. C., and T. Pipan. 2019. *The Biology of Caves and Other Subterranean Habitats*. 2nd ed. New York: Oxford University Press.
- Di Cola, V., O. Broennimann, B. Petitpierre, et al. 2017. "Ecospat: An R Package to Support Spatial Analyses and Modeling of Species Niches and Distributions." *Ecography* 40: 774–787.
- Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36: 27–46.
- Elith, J., and J. R. Leathwick. 2009. "Species Distribution Models: Ecological Explanation and Prediction Across Space and Time." *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.
- Ficetola, G. F., E. Lunghi, C. Canedoli, E. Padoa-Schioppa, R. Pennati, and R. Manenti. 2018. "Differences Between Microhabitat and Broad-Scale Patterns of Niche Evolution in Terrestrial Salamanders." *Scientific Reports* 8: 10575.
- Ficetola, G. F., E. Lunghi, R. Cimmaruta, and R. Manenti. 2019. "Transgressive Niche Across a Salamander Hybrid Zone Revealed by Microhabitat Analyses." *Journal of Biogeography* 46: 1342–1354.
- Ficetola, G. F., and L. Maiorano. 2016. "Contrasting Effects of Temperature and Precipitation Change on Amphibian Phenology, Abundance and Performance." *Oecologia* 181: 683–693.
- Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.
- Foden, W. B., S. H. M. Butchart, S. N. Stuart, et al. 2013. "Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals." *PLoS One* 8: e65427.
- Ginal, P., C.-H. Loske, T. Hörren, and D. Rödder. 2021. "Cave Salamanders (*Speleomantes* spp.) in Germany: Tentative Species Identification, Estimation of Population Size and First Insights Into an Introduced Salamander." *Herpetology Notes* 14: 815–822.
- Grant, E. H. C., D. A. Miller, B. R. Schmidt, et al. 2016. "Quantitative Evidence for the Effects of Multiple Drivers on Continental-Scale Amphibian Declines." *Scientific Reports* 6: 1–9.
- Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. *Habitat Suitability and Distribution Models: With Applications in R*. United Kingdom: Cambridge University Press, University Printing House, Cambridge CB2 8BS.
- Hijmans, R. J., and J. Elith. 2016. *Dismo-Package: Species Distribution Modeling With R. R Package Version 1.1-1*. <https://CRAN.R-project.org/package=dismo>.
- Hill, J. K., H. M. Griffiths, and C. D. Thomas. 2011. "Climate Change and Evolutionary Adaptations at species' Range Margins." *Annual Review of Entomology* 56: 143–159.
- Howarth, F. G., and O. T. Moldovan. 2018. "The Ecological Classification of Cave Animals and Their Adaptations." In *Cave Ecology*, edited by O. T. Moldovan, L. Kováč, and S. Halse, 41–67. Berlin: Springer.
- Iannella, M., F. Cerasoli, and M. Biondi. 2017. "Unraveling Climate Influences on the Distribution of the Parapatric Newts *Lissotriton vulgaris Meridionalis* and *L. italicus*." *Frontiers in Zoology* 14: 1–14.
- Iannella, M., P. D'Alessandro, and M. Biondi. 2018. "Evidences for a Shared History for Spectacled Salamanders, Haplotypes and Climate." *Scientific Reports* 8: 1–11.
- IUCN SSC Amphibian Specialist Group. 2022a. "*Speleomantes ambrosii*. The IUCN Red List of Threatened Species 2022: e.T20454A89708811." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20454A89708811.en>.
- IUCN SSC Amphibian Specialist Group. 2022b. "*Speleomantes italicus*. The IUCN Red List of Threatened Species 2022: e.T20458A89709054." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20458A89709054.en>.
- IUCN SSC Amphibian Specialist Group. 2022c. "*Speleomantes strinatii*. The IUCN Red List of Threatened Species 2022: e.T59405A89709164." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T59405A89709164.en>.
- IUCN SSC Amphibian Specialist Group. 2022d. "*Speleomantes flavus*. The IUCN Red List of Threatened Species 2022: e.T20455A89699228." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20455A89699228.en>.
- IUCN SSC Amphibian Specialist Group. 2022e. "*Speleomantes genei*. The IUCN Red List of Threatened Species 2022: e.T20456A89697852." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20456A89697852.en>.
- IUCN SSC Amphibian Specialist Group. 2022f. "*Speleomantes imperialis*. The IUCN Red List of Threatened Species 2022: e.T20457A89708919." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20457A89708919.en>.
- IUCN SSC Amphibian Specialist Group. 2022g. "*Speleomantes sarra-busensis*. The IUCN Red List of Threatened Species 2022: e.T135825A89699335." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T135825A89699335.en>.
- IUCN SSC Amphibian Specialist Group. 2022h. "*Speleomantes supramontis*. The IUCN Red List of Threatened Species 2022: e.T20459A89697409." <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T20459A89697409.en>.
- Lanza, B., C. Pastorelli, P. Laghi, and R. Cimmaruta. 2006. "A Review of Systematics, Taxonomy, Genetics, Biogeography and Natural

- History of the Genus *Speleomantes* Dubois, 1984 (Amphibia Caudata Plethodontidae).” *Atti del Museo Civico di Storia Naturale di Trieste* 52: 5–135.
- Liu, C., M. White, and G. Newell. 2013. “Selecting Thresholds for the Prediction of Species Occurrence With Presence-Only Data.” *Journal of Biogeography* 40: 778–789.
- Lowe, W. H. 2011. “Climate Change Is Linked to Long-Term Decline in a Stream Salamander.” *Biological Conservation* 145: 48–53.
- Lucente, D., J. Renet, M. Gaillardat, J. Tillet, G. Nascetti, and R. Cimmaruta. 2016. “A New Population of European Cave Salamanders (Genus *Hydromantes*) From West-Central France: Relict or Introduction?” *Herpetological Bulletin* 138: 21–23.
- Luedtke, J. A., J. Chanson, K. Neam, et al. 2023. “Ongoing Declines for the world’s Amphibians in the Face of Emerging Threats.” *Nature* 622, no. 7982: 308–314.
- Lunghi, E. 2022. “Doubling the Lifespan of European Plethodontid Salamanders.” *Ecology* 103: e03581.
- Lunghi, E., and G. Bruni. 2018. “Long-Term Reliability of Visual Implant Elastomers in the Italian Cave Salamander (*Hydromantes italicus*).” *Salamandra* 54: 283–286.
- Lunghi, E., F. Cianferoni, F. Ceccolini, et al. 2018. “Field-Recorded Data on the Diet of Six Species of European *Hydromantes* Cave Salamanders.” *Scientific Data* 5: 180083.
- Lunghi, E., F. Cianferoni, C. Corti, et al. 2022. “The Trophic Niche of Subterranean Populations of *Speleomantes italicus*: A Multi-Temporal Analysis.” *Scientific Reports* 12: 18257.
- Lunghi, E., C. Corti, R. Manenti, et al. 2018. “Comparative Reproductive Biology of European Cave Salamanders (Genus *Hydromantes*): Nesting Selection and Multiple Annual Breeding.” *Salamandra* 54: 101–108.
- Lunghi, E., C. Corti, R. Manenti, and G. F. Ficetola. 2019. “Consider Species Specialism When Publishing Datasets.” *Nature Ecology & Evolution* 3: 319.
- Lunghi, E., R. Manenti, G. Canciani, G. Scari, R. Pennati, and G. F. Ficetola. 2016. “Thermal Equilibrium and Temperature Differences Among Body Regions in European Plethodontid Salamanders.” *Journal of Thermal Biology* 60: 79–85.
- Lunghi, E., R. Manenti, and R. Cimmaruta. 2022. “The Identity of an Allochthonous Pyrenean Population of *Speleomantes* Cave Salamanders.” *Salamandra* 58: 67–70.
- Lunghi, E., R. Manenti, and G. F. Ficetola. 2015. “Seasonal Variation in Microhabitat of Salamanders: Environmental Variation or Shift of Habitat Selection?” *PeerJ* 3: e1122.
- Lunghi, E., R. Manenti, M. Mulargia, M. Veith, C. Corti, and G. F. Ficetola. 2018. “Environmental Suitability Models Predict Population Density, Performance and Body Condition for Microendemic Salamanders.” *Scientific Reports* 8: 7527.
- Maia-Carvalho, B., C. G. Vale, F. Sequeira, N. Ferrand, I. Martinez-Solano, and H. Gonçalves. 2018. “The Roles of Allopatric Fragmentation and Niche Divergence in Intraspecific Lineage Diversification in the Common Midwife Toad (*Alytes obstetricans*).” *Journal of Biogeography* 45: 2146–2158.
- Mammola, S., S. L. Goodacre, and M. Isaia. 2018. “Climate Change May Drive Cave Spiders to Extinction.” *Ecography* 41: 233–243.
- Mammola, S., E. Piano, P. Cardoso, et al. 2019. “Climate Change Going Deep: The Effects of Global Climatic Alterations on Cave Ecosystems.” *Anthropocene Review* 6: 98–116.
- Martel, A., A. Spitzen-van der Sluijs, M. Blooi, et al. 2012. “*Batrachochytrium Salamandrivorans* sp. nov. Causes Lethal Chytridiomycosis in Amphibians.” *Proceedings of the National Academy of Sciences of the United States of America* 110: 15325–15329.
- Min, M. S., S. Y. Yang, R. M. Bonett, D. R. Vieites, R. A. Brandon, and D. B. Wake. 2005. “Discovery of the First Asian Plethodontid Salamander.” *Nature* 435: 87–90.
- Naimi, B., N. A. Hamm, T. A. Groen, A. K. Skidmore, and A. G. Toxopeus. 2014. “Where Is Positional Uncertainty a Problem for Species Distribution Modelling?” *Ecography* 37: 191–203.
- Pabijan, M., G. Palomar, B. Antunes, W. Antoń, P. Zieliński, and W. Babik. 2020. “Evolutionary Principles Guiding Amphibian Conservation.” *Evolutionary Applications* 13: 857–878.
- Pauls, S. U., C. Nowak, M. Bálint, and M. Pfenninger. 2013. “The Impact of Global Climate Change on Genetic Diversity Within Populations and Species.” *Molecular Ecology* 22: 925–946.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. “Maximum Entropy Modeling of Species Geographic Distributions.” *Ecological Modelling* 190, no. 3–4: 231–259.
- Pittman, S. E., M. S. Osbourn, and R. D. Semlitsch. 2013. “Movement Ecology of Amphibians: A Missing Component for Understanding Population Declines.” *Biological Conservation* 169: 44–53.
- Pough, F. H., R. M. Andrews, M. L. Crump, A. H. Savitzky, K. D. Wells, and M. C. Brandley. 2016. *Herpetology*. 4th ed. Sunderland, MA: Sinauer Associates, Inc.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Raes, N., and H. ter Steege. 2007. “A Null-Model for Significance Testing of Presence-Only Species Distribution Models.” *Ecography* 30: 727–736.
- Riahi, K., D. P. Van Vuuren, E. Kriegler, et al. 2017. “The Shared Socioeconomic Pathways and Their Energy, Land Use, and Greenhouse Gas Emissions Implications: An Overview.” *Global Environmental Change* 42: 153–168.
- Rizzo, V., D. Sánchez-Fernández, J. Fresneda, A. Cieslak, and I. Ribera. 2015. “Lack of Evolutionary Adjustment to Ambient Temperature in Highly Specialized Cave Beetles.” *BMC Evolutionary Biology* 15: 10.
- Rondinini, C., A. Battistoni, and C. Teofili. 2022. *Lista Rossa IUCN dei vertebrati italiani 2022*. Roma: Comitato Italiano IUCN e Ministero dell’Ambiente e della Sicurezza Energetica.
- Salvidio, S. 2013. “Homing Behaviour in *Speleomantes strinatii* (Amphibia Plethodontidae): A Preliminary Displacement Experiment.” *North-Western Journal of Zoology* 9: 429–433.
- Salvidio, S., A. Latters, M. Tavano, F. Melodia, and M. V. Pastorino. 1994. “Ecology of a *Speleomantes ambrosii* Population Inhabiting an Artificial Tunnel.” *Amphibia-Reptilia* 15: 35–45.
- Sánchez-Fernández, D., V. Rizzo, A. Cieslak, A. Faille, J. Fresneda, and I. Ribera. 2016. “Thermal Niche Estimators and the Capability of Poor Dispersal Species to Cope With Climate Change.” *Scientific Reports* 6: 23381.
- Schulz, V., P. Gerhardt, D. Stützer, U. Seidel, and M. Vences. 2021. “Lungless Salamanders of the Genus *Speleomantes* in the Solling, Germany: Genetic Identification, *Bd/Bsal*-Screening, and Introduction Hypothesis.” *Herpetology Notes* 14: 421–429.
- Shen, X.-X., D. Liang, M.-Y. Chen, R.-L. Mao, D. B. Wake, and P. Zhang. 2016. “Enlarged Multilocus Data Set Provides Surprisingly Younger Time of Origin for the Plethodontidae, the Largest Family of Salamanders.” *Systematic Biology* 65: 66–81.
- Sillero, N. 2011. “What Does Ecological Modelling Model? A Proposed Classification of Ecological Niche Models Based on Their Underlying Methods.” *Ecological Modelling* 222: 1343–1346.
- Sillero, N., S. Arenas-Castro, U. Enriquez-Urzelai, et al. 2021. “Want to Model a Species Niche? A Step-By-Step Guideline on Correlative Ecological Niche Modelling.” *Ecological Modelling* 456: 109671.

- Sillero, N., and A. M. Barbosa. 2021. "Common Mistakes in Ecological Niche Models." *International Journal of Geographical Information Science* 35: 1–14.
- Spotila, J. R. 1972. "Role of Temperature and Water in the Ecology of Lungless Salamanders." *Ecological Monographs* 42: 95–125.
- Stralberg, D., S. Matsuoka, A. Hamann, et al. 2015. "Projecting Boreal Bird Responses to Climate Change: The Signal Exceeds the Noise." *Ecological Applications* 25: 52–69.
- Stuart, S. N., J. S. Chanson, N. A. Cox, et al. 2004. "Status and Trends of Amphibian Declines and Extinctions Worldwide." *Science* 306: 1783–1786.
- Tatebe, H., T. Ogura, T. Nitta, et al. 2019. "Description and Basic Evaluation of Simulated Mean State, Internal Variability, and Climate Sensitivity in MIROC6." *Geoscientific Model Development* 12: 2727–2765.
- Thuiller, W., D. Georges, and R. Engler. 2023. "biomod2: Ensemble Platform for Species Distribution Modeling. R Package Version 3.3-7." <http://CRAN.R-project.org/package=biomod2>.
- Visser, M. E. 2008. "Keeping Up With a Warming World; Assessing the Rate of Adaptation to Climate Change." *Proceedings of the Royal Society B* 275: 649–659.
- Wake, D. B. 2013. "The Enigmatic History of the European, Asian and American Plethodontid Salamanders." *Amphibia-Reptilia* 34: 323–336.
- Wróblewska, A., and P. Mirski. 2018. "From Past to Future: Impact of Climate Change on Range Shifts and Genetic Diversity Patterns of Circumboreal Plants." *Regional Environmental Change* 18: 409–424.
- Wu, T., Y. Lu, Y. Fang, et al. 2019. "The Beijing Climate Center Climate System Model (BCC-CSM): The Main Progress From CMIP5 to CMIP6." *Geoscientific Model Development* 12: 1573–1600.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.