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Dark future for a black salamander: effects of climate change and conservation implications for an endemic alpine amphibian

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Climate change is threatening several montane species across the world, including a large number of endemics, needing the development of forward-looking conservation strategies to foster their future survival. In this context, Species Distribution Models (SDMs) represent a useful method to forecast changes in species' habitat suitability under different scenarios of global warming, often advising conservation frameworks with credible, defensible and repeatable information. In this paper, we estimate the environmental and bioclimatic suitability for an endemic mountain amphibian (*Salamandra lanzai*) in the western European Alps through an SDM approach, considering both current and future scenarios, to address short- and long-term management and conservation actions, and to update the current IUCN extinction risk assessment. The ensemble model forecasts predict a dramatic decline of the climatically suitable area for the Lanza's alpine salamander in the next 20–40 years, even considering an optimistic CO_2 emissions scenario, leading to a theoretical extinction of this species in 2100 in case the worst global warming prediction will be actualised. This underlines the urgent need for up-to-date conservation and management strategies to ensure the successful mitigation of climate change effects on *S. lanzai*, especially by adapting and improving the network of protected areas, immediately removing additional threats and identifying possible management actions able to increase fine-scale habitat suitability and connectivity among populations. In addition, a significant range contraction in the future has to be considered when assessing the extinction risk for this species, possibly exacerbating the effect of other threatening factors, such as the spread of lethal pathogens.

Keywords: Salamandra lanzai, ensemble models, environmental suitability, bioclimatic suitability, future projections

INTRODUCTION

Climate change is threatening biodiversity worldwide and the number of species under extinction risk is expected to steeply increase with the rise of global temperatures in the near future (IPCC, 2022). In this context, mountain systems represent one of the most vulnerable ecosystems (Chakraborty, 2021; Schmeller et al., 2022), not only because they host a significant proportion of the global biological diversity (Körner & Spehn, 2002; Perrigo et al., 2020), but most importantly because average air temperatures at high elevations proved to increase faster than the overall global warming rate in the last decades (IPCC, 2018). Accordingly, several montane species are requiring attention from a conservation point of view (especially endemics, Manes et al., 2021), needing the development of forward-looking management strategies able to foster their resilience and adaptation to climate change, even anticipating future distribution and habitat suitability shifts (Clark et al., 2001; Tulloch et al., 2020).

Species Distribution Models (SDMs) are a widely used method to project species distributions in space and time under climate change (Araújo et al., 2019), often advising conservation frameworks with credible, defensible and repeatable information (Sofaer et al., 2019). In their most common correlative form, SDMs typically use the known locations of a given taxon and information on the corresponding environmental conditions to produce habitat suitability maps (Peterson et al., 2011), which can be also projected in the future according to the available climatic and environmental scenarios, allowing to detect possible species range shifts/expansions/contractions through time (Yalcin & Leroux, 2017), to inform extinction risk assessments (Syfert et al., 2014), and to address biodiversity conservation efforts (Guisan et al., 2013).

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Since amphibians show the highest proportion of threatened species among the world's vertebrates (Hoffmann et al., 2010), with climate change representing one of major drivers for the decline of many taxa (Blaustein et al., 2010), SDMs are a frequently used approach to predict future distributions within this animal group. In particular, a number of modelling attempts (e.g. Cordier et al., 2020; Feldmeier et al., 2020; Jacobsen et al., 2020; Lyons & Kozak, 2020; Dubos et al., 2023) have been focused on high-elevation species, which are expected to be particularly sensitive to climatic alterations due to their special adaptations to relatively low temperatures, restricted activity periods and intermittent water availability.

The Lanza's alpine salamander *Salamandra lanzai* (Nascetti et al., 1988) is one of the few amphibians that successfully colonise alpine habitats in the European Alps, thanks to several biological, physiological, ecological, and behavioural traits. In particular, this urodele emancipated from water for reproduction, evolving an aplacental viviparous strategy that allows for better offspring thermoregulation, while ensuring food availability through oophagy or adelphophagy (Bovero et al., 2013). In addition, this species is able to continuously track suitable climatic conditions by alternating epigean and hypogean phases, with surface-dwelling individuals becoming visible only on relatively humid nights and on rainy days between April and October (Andreone et al., 1999a). Accordingly, the Lanza's alpine salamander leads a predominantly subterranean life (Andreone, 2006), benefiting from the relatively stable microclimatic conditions of the underground network of cracks and crevices (Ribéron & Miaud, 2000; Mammola et al., 2016), the so-called Milieu Souterrain Superficiel (MSS; Culver & Pipan, 2014), which also provides a suitable habitat for hibernation and for young salamanders' growth until sexual maturity (Andreone, 2006). Above ground, alpine grassland and shrubland habitats surrounded or interspersed by rocks and screes are usually preferred by this species (Abdulhak, 2016, unpublished report), with only some populations living in larch woodlands (Andreone, 2006).

Sedentarity is another important feature of *S. lanzai*'s ecology: radio-tracked adults showed a rather limited dispersal capacity, with a mean home range of about 50 m^2 exploited in a 4-week period (Ribéron & Miaud, 2000), while cumulative movements of a few hundreds of metres (< 400 m) each year can be inferred from capture-mark-recapture observations (Andreone et al., 1999a). Surface activity is thus probably dedicated mainly to feed on ground-dwelling insects (Andreone et al., 1999b), as well as to the search for mating partners (Andreone, 1992). However, despite very limited daily or inter-annual movements, the Lanza's alpine salamander is characterised by an inter-generational dispersal over long distances, as highlighted by its genetic structuring, revealing the progressive colonisation of relatively far new favourable areas among generations, starting from several refugia where populations became isolated during the last glacial maximum (Montgelard et al., under review).

S*alamandra lanzai* is subjected to a rigorous protection in the European Union (EU Directive 92/43/EEC, Annex IV) and it is classified as Critically Endangered by the International Union for Conservation of Nature (IUCN), in view of its restricted distribution (West-Alpine endemic) and the predicted spread of the lethal fungal pathogen *Batrachochytrium salamandrivorans* (*Bsal*), which has more than 50 % probability to cause the extinction of this species in the next 45 years (IUCN SSC Amphibian Specialist Group, 2022). In addition, populations are inferred to be locally decreasing, owing to the localised decline in habitat extent and quality, and to the severe impact of road mortality in some areas (IUCN SSC Amphibian Specialist Group, 2022). Surprisingly, the IUCN assessment does not mention climatic variations as a possible additional factor that could compromise the survival of this salamander in the future, likely because future projections on the distribution of this endemic urodele are still lacking (but see Dubos et al., 2023), preventing the availability of reliable data to support extinction risk evaluations across different climate change scenarios and time periods.

In order to fill this information gap, this study applies an SDM approach to map the current and future environmental and bioclimatic suitability for the Lanza's alpine salamander throughout its range. The first aim is to identify the main environmental and bioclimatic variables currently correlated with the distribution of *S. lanzai*, then projecting them in space, in order to outline the suitable area where further research can be performed, and where to focus short-term management and conservation actions. Furthermore, this study aims to project the bioclimatic suitability for this urodele in the future, in order to forecast if and how the extent of the suitable area will change in the next century, due to rising temperatures and the expected changes in precipitation regimes, possibly providing useful information to update the current IUCN extinction risk assessment and for long-term conservation planning (e.g. improvement of the current protected areas network).

MATERIALS & METHODS

Calibration area, occurrence data and predictors

Models were calibrated within a rectangular area encompassing all the known range of *S. lanzai* in the western European Alps (3433 km^2), between Italy and France (Fig. 1; Appendix S1.1). In this area, 360 geo-referenced occurrence points were selected for the modelling procedure (Fig. 1), starting from a raw database of 3382 spatially-autocorrelated records (see Appendix S1.2). In particular, data were first sorted temporally (focusing on the 2000–2021 period) and then spatially (one record per ~150 m pixel, in accordance with predictors' resolution).

In a first model arrangement (hereafter defined as "environmental suitability model"), the total solar radiation in June (Srad06), the minimum temperature of the coldest month (Bio06), total annual precipitations (Bio12), the Normalised Difference Vegetation Index (NDVI) values of July (NDVI07) and the mean temperature of the driest quarter of the year (Bio09) were selected among an initial

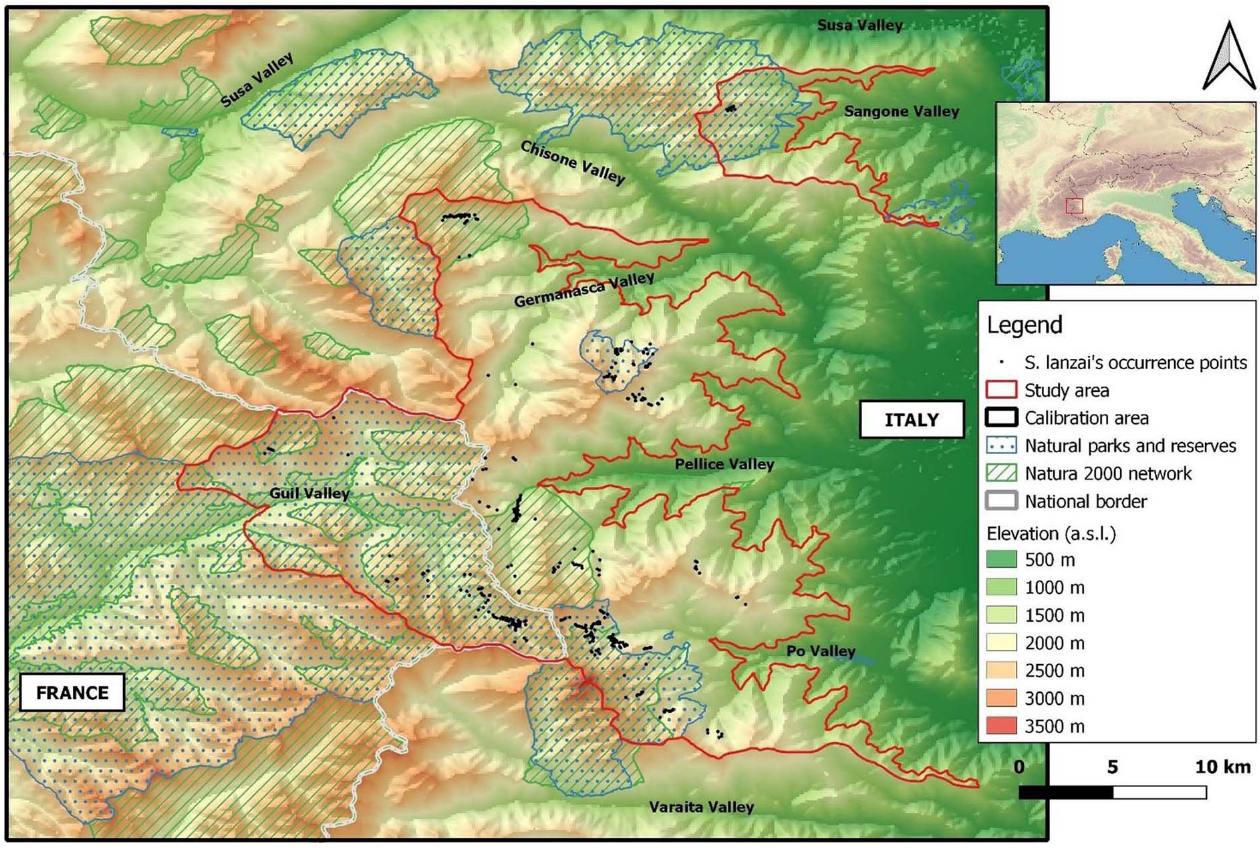

Figure 1. Map of the calibration area (black box), in which the perimeter of the subset study area is highlighted in red. Black dots represent the Lanza's alpine salamander's occurrences used to calibrate the models (N = 360). The extent of Natura 2000 sites (in green) and natural parks and reserves (in blue) is also reported. The Digital Terrain Model (DTM) provides the baseline map.

array of 25 topographic, bioclimatic and environmental predictors (Table 1; resolution: ~150 m, see Appendix S1.4), after evaluating the inter-correlation between parameters and the relative importance of each variable (Appendix S1.3). Secondly, since future projections are available only for temperature and precipitations data, a further variable selection procedure was carried out considering only bioclimatic and topographic predictors (the latter assumed to be constant through time), in order to allow the calibration of an additional "bioclimatic suitability model", required as a preparatory step to run future predictions. In this case, the minimum temperature of the coldest month (Bio06), precipitation seasonality (Bio15), total annual precipitations (Bio12) and mean temperature of the driest quarter of the year (Bio09) were the selected parameters.

Future projections of Bio06, Bio09, Bio12 and Bio15 were obtained from the CMIP6 downscaled future climate projections, according to three Global Circulation Models (GCMs) (ACCESS-ESM1-5; MPI-ESM1-2-HR; MIROC6) and two Shared Socio-economic Pathways (SSPs; Meinshausen et al., 2020) (SSP126, low CO_2 emissions; SSP585, high CO_2 emissions) in two time periods (short-term, 2041–2060; long-term, 2081–2100) (see Appendix S1.3). Accordingly, 12 different projections of the selected variables were considered to predict the future bioclimatic suitability for the Lanza's alpine salamander (i.e. 3 GCMs x 2 SSPs x 2 time periods).

Modelling procedure

An ensemble forecasting method (Araújo & New, 2007) was applied to model the environmental and bioclimatic suitability for *S. lanzai* within the calibration area, involving eight widely-used niche-based algorithms, all available in the biomod2 package (ver. 4.2.2; Thuiller et al., 2023) in R (ver. 4.2.2; R Core Team, 2022): Generalized Boosting Model (GBM; Ridgeway, 1999), Classification Tree Analysis (CTA; Breiman et al., 1984), Flexible Discriminant Analysis (FDA; Hastie et al., 1994), Generalized Additive Models (GAM; Hastie & Tibshirani, 1990), Generalized Linear Models (GLM; McCullagh & Nelder, 1989), MaxEnt (MXT; Phillips et al., 2006), Multiple Adaptive Regression Splines (MARS; Friedman, 1991) and Random Forest (RF; Breiman, 2001). All the algorithms were run 10 times, each one corresponding to a randomly-selected series of 500 pseudo-absence points throughout the calibration area. A spatial block cross-validation strategy (Muscarella et al., 2014) was applied to test models' predictive power, then quantified by means of two evaluation metrics: the true skill statistic (TSS; Allouche et al., 2006) and the area under the relative operating characteristic curve (AUC; Fielding & Bell, 1997). Model robustness was evaluated five times per algorithm in each one of the ten performed runs, in order to obtain an average value of model performances, and the final models were calibrated on 100 % of the data. Then, the response of the Lanza's alpine salamander to each predictor was evaluated by applying the evaluation strip method proposed by Elith et al. (2005).

Table 1. List of the 25 candidate predictors considered in the first phase of the modelling process regarding *S. lanzai*. For each predictor type, all variables are listed reporting their code, a short description and the data source (SRTM = Shuttle Radar Topography Mission). The parameters selected for the final model calibration (ESM = environmental suitability model; BSM = bioclimatic suitability model) are highlighted in bold.

Type	Code	Description	ESM	BSM	Source
Topographic	DTM	Elevation			SRTM (Farr et al., 2007)
	Exp	Exposition			SRTM (Farr et al., 2007)
	Slo	Slope			SRTM (Farr et al., 2007)
	TPI	Topographic Position Index			SRTM (Farr et al., 2007)
Bioclimatic	Bio01	Mean annual temperature			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio02	Mean diurnal range			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio03	Isothermality			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio04	Temperature seasonality			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio05	Max temperature of warmest month			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio06	**Min temperature of coldest month**	**X**	**X**	WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio07	Temperature annual range			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio08	Mean temperature of the wettest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio09	**Mean temperature of driest quarter**	**X**	**X**	WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio10	Mean temperature of warmest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio11	Mean temperature of coldest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio12	**Total annual precipitation**	**X**	**X**	WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio13	Precipitation of wettest month			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio14	Precipitation of driest month			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio15	**Precipitation seasonality**		**X**	WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio16	Precipitation of wettest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio17	Precipitation of driest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio18	Precipitation of warmest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Bio19	Precipitation of coldest quarter			WorldClim 2.1 (Fick & Hijmans, 2017)
	Srad06	**Total solar radiation June**	**X**		WorldClim 2.1 (Fick & Hijmans, 2017)
Environmental	**NDVI07**	**NDVI July**	**X**		MOD13A3.061 (Didan, 2021)

Model runs with TSS values below 0.7 were discarded from the ensemble forecasting procedure, with consensus distributions resulting from the averaging of model predictions, proportionally weighted basing on their TSS evaluation. Final environmental and bioclimatic suitability maps were then obtained by averaging ensemble forecasts from the ten pseudo-absence runs. In addition, the original suitability maps were transformed into maps of suitable vs unsuitable areas (binary maps), by choosing the occurrence probability threshold that maximised the TSS value (Liu et al., 2005; Jiménez-Valverde & Lobo, 2007).

Future predictions were built starting from the current bioclimatic suitability model outputs, but considering the future projections of Bio06, Bio09, Bio12 and Bio15 as predictors. Firstly, three bioclimatic suitability maps and three binary maps were generated per time period and per SSP, according to the future predictions provided by the three GCMs considered. Then, final maps (N = 4, one per time period and per SSP) were obtained by averaging the results from the three GCMs. In the final binary maps, presence was attributed where the majority of GCMs (i.e. two out of three) predicted presence, otherwise attributing absence.

Model validation in the field

In addition to the statistical model performance evaluation, targeted field surveys were carried out within the calibration area by well-trained operators (D.S., P.E.B., R.C., M.F. & D.G.), in order to verify the actual occurrence of *S. lanzai* in the suitable areas predicted by the ensemble models for the current scenario. In particular, previously little-explored areas were selected for surveys, profiting from model outputs to search for possible new populations or to highlight local inconsistencies in predictions.

Between June and early September 2022, nine sectors of the calibration area (Fig. 2) were inspected following a standard monitoring protocol, based on visual encounter surveys in two sampling sessions per area. Each survey was carried out in rainy days and/or by night, searching for surface-dwelling Lanza's alpine salamanders in their typical habitats. The explored area was tracked with a GPS, georeferencing each observation, while if no individuals were found in both sampling sessions, the species was considered as absent from the surveyed sector.

Spatial analyses

In order to obtain quantitative data from the ensemble model outputs, some spatial analyses were performed on the final suitability maps, focusing in particular on binary

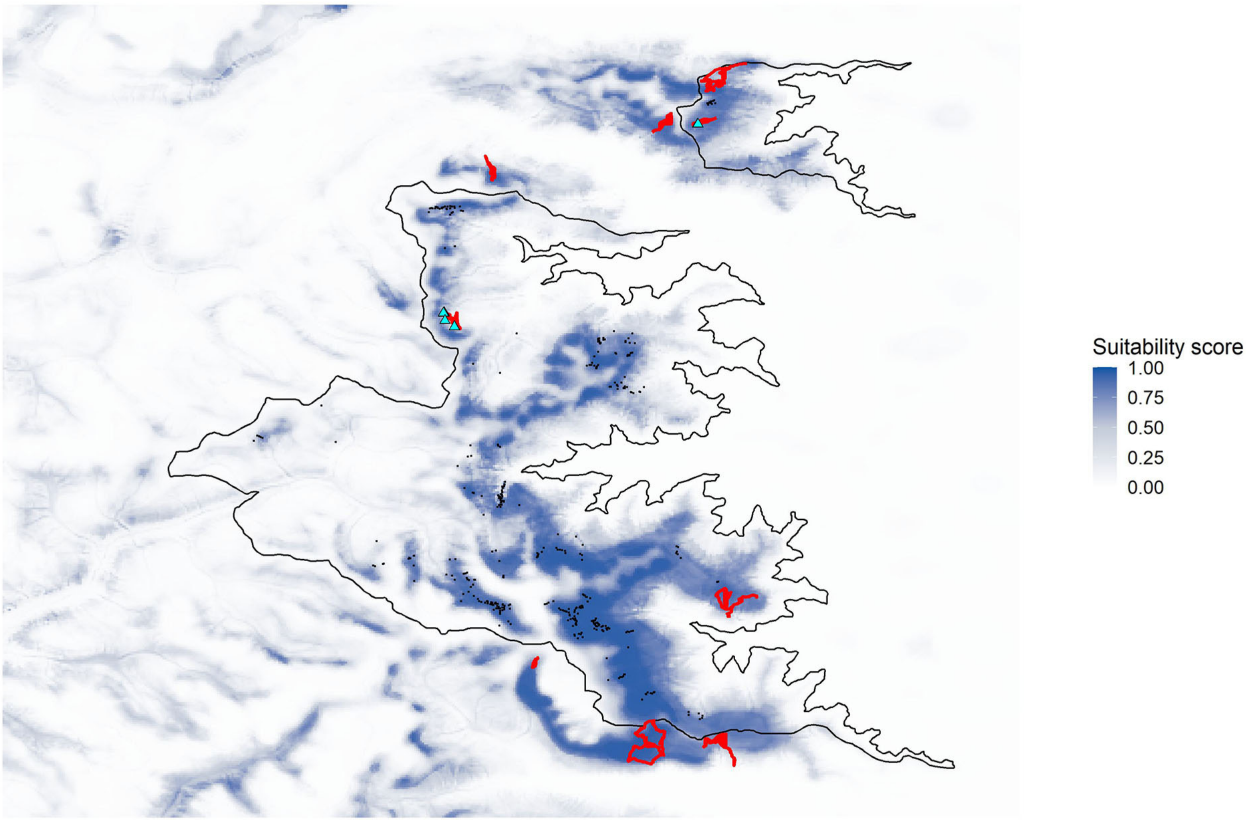

Figure 2. Map reporting the GPS tracks (in red) recorded during the targeted surveys carried out to validate the ensemble model results in the field. The light-blue triangles highlight the new occurrence points of *S. lanzai* resulting from these surveys (N = 14). Black dots represent the Lanza's alpine salamander's occurrences used to calibrate the models (N = 360), while the black line identifies the perimeter of the study area considered in spatial analyses. The baseline map reports the suitable area for *S. lanzai*, as predicted by the environmental suitability model.

maps. Since occurrence data and targeted field surveys proved that the current distribution of *S. lanzai* actually covers only a portion of the overall predicted suitable area, spatial analyses were carried out considering a subset area (assumed to correspond to the G_0 area, sensu Peterson et al., 2011; hereafter "study area"; 778 km^2, Fig. 1), outlined within the calibration area following an expert-based approach (Appendix S1.1).

The binary maps cropped on the study area were used to calculate the predicted extent of the suitable area for *S. lanzai*, its overlap with protected areas (i.e. natural parks, natural reserves and Natura 2000 sites) and the potential elevation range, also highlighting future variations based on the two SSP and the two time periods considered in the modelling procedure. Moreover, two additional distribution parameters (extent of occurrence, EOO; area of occupancy, AOO) were calculated by means of the red package (ver. 1.5.0; Cardoso, 2020) in R (R Core Team, 2022), in accordance with the guidelines to assess species' extinction risk provided by the International Union for Conservation of Nature (IUCN Standards and Petitions Committee, 2022).

RESULTS

Model performance

Most of the algorithms involved in the environmental suitability model showed a good performance, with an average TSS of 0.832 ± 0.079 and a mean AUC of 0.955 ± 0.034. RF is the modelling technique that performed better, followed by GBM and CTA, while GAM and GLM showed the worst predictive power. Similar results in terms of model performance were obtained by the bioclimatic suitability model (mean TSS: 0.788 ± 0.011; mean AUC: 0.942 ± 0.044), with RF as best performing algorithm, followed by GBM, CTA, and MXT (Table 2).

According to the fitted response curves (Fig. S2.1, S2.2), the probability of occurrence of *S. lanzai* within the calibration area is highest where the total solar radiation in June (Srad06) is about 23000 Kj/m^2, where the minimum temperature of the coldest month of the year (Bio06) is about -9 °C, where NDVI values in July (NDVI07) fall between 0.40 and 0.65, where the mean temperature of the driest quarter of the year exceeds 11 °C and where precipitations show a relatively low variability throughout the year (Bio15 = 17–20 %). A bimodal response is highlighted concerning the annual precipitations (Bio12), with the highest probability of occurrence at 800 mm and 1200 mm.

Current potential Lanza's alpine salamander distribution

According to the environmental suitability model, the current potential range of *S. lanzai* in the study area covers 226 km^2 (Fig. 3a–c), with a mean elevation of 2159 ± 250 m a.s.l. The core suitable area is located around the Monviso massif, extending in particular in the upper Po, Pellice and

Table 2. Evaluation metrics (mean ± standard deviation) concerning the environmental and bioclimatic suitability models, calculated for each one of the eight algorithms considered in the ensemble modelling procedure (TSS = true skill statistic; AUC = area under the relative operating characteristic curve). Algorithms are listed in alphabetical order (CTA = Classification Tree Analysis; FDA = Flexible Discriminant Analysis; GAM = Generalized Additive Models; GBM = Generalized Boosting Model; GLM = Generalized Linear Models; MARS = Multiple Adaptive Regression Splines; MXT = MaxEnt; RF = Random Forest).

Algorithm	Environmental suitability model		Bioclimatic suitability model	
	TSS	AUC	TSS	AUC
CTA	0.855 ± 0.036	0.956 ± 0.020	0.847 ± 0.038	0.954 ± 0.021
FDA	0.793 ± 0.029	0.952 ± 0.010	0.727 ± 0.046	0.926 ± 0.013
GAM	0.767 ± 0.072	0.919 ± 0.052	0.670 ± 0.097	0.879 ± 0.069
GBM	0.882 ± 0.017	0.987 ± 0.003	0.865 ± 0.023	0.978 ± 0.006
GLM	0.760 ± 0.038	0.935 ± 0.021	0.700 ± 0.065	0.920 ± 0.020
MARS	0.806 ± 0.029	0.957 ± 0.009	0.748 ± 0.047	0.935 ± 0.013
MXT	0.810 ± 0.032	0.936 ± 0.017	0.766 ± 0.047	0.944 ± 0.020
RF	0.987 ± 0.004	1.000 ± 0.000	0.983 ± 0.006	1.000 ± 0.000

Guil valleys. This area is in connection northwards with other suitable patches located in the upper Germanasca Valley, constituting a continuous suitable range until the Albergian massif. Conversely, the environmental suitability for the Lanza's alpine salamander appears to be more fragmented in the westernmost part of its range, with a single isolated patch identified in the Malrif area. Then, the model also predicts a disjunct suitable area in the upper Sangone Valley.

The 47.8 % (108 km^2) of the environmentally suitable area currently overlaps with protected areas, with the Natura 2000 network contributing in *S. lanzai*'s protection on 86 km^2 (38.0 %), while natural parks and reserves cover 75 km^2 (33.2 %) of the potential species range within the study area. According to the IUCN criteria and basing on the environmental model outputs, the extent of occurrence (EOO) of the Lanza's alpine salamander covers 1058 km^2, while the area of occupancy (AOO) extends for 560 km^2.

Similar results in terms of core range were obtained by running the bioclimatic suitability model, although the outputs proved to be less conservative than the environmental ones in the study area, predicting a climatically suitable area of 274 km^2 (+21.2 %) (Fig. 3b–d). In particular, this model partly extends the current predicted range of *S. lanzai* towards lower elevations (mean = 2136 ± 262 m). However, more than two-thirds (70.4 %; 193 km^2) of the climatically suitable area overlap with the potential range identified by the environmental suitability model, which in turn is mostly a subset of the eligible area from a bioclimatic point of view (i.e. 85.4 % of overlap).

The suitable area outlined by the bioclimatic suitability model overlaps with protected areas on 114 km^2 (41.6 %), showing also in this case a major contribution of Natura 2000 sites (88 km^2; 32.1 %), while 80 km^2 (29.2 %) are covered by natural parks and reserves. The predicted bioclimatic EOO is 959 km^2, encompassing an AOO of 656 km^2.

Model validation in the field

Overall, during the targeted field surveys 108 km were walked within the suitable area predicted by the ensemble model. However, the occurrence of the Lanza's alpine salamander was confirmed in only two of the nine inspected sectors, namely the Balma Valley (Sangone Valley) and the Rodoretto Valley (Germanasca Valley) (Fig. 2). In particular, only two individuals were observed in the Balma Valley, while a relatively abundant population was detected in the Rodoretto Valley (N = 12). Despite the predicted high environmental suitability, *S. lanzai* appears to be absent in the Chisone Valley and on the southern slope of the Monviso massif (Varaita Valley).

Future scenarios

The future projections of the bioclimatic suitability model forecast a dramatic reduction and fragmentation of the climatically suitable area for *S. lanzai*, especially in the western and northern portions of its range, with considerable effects already predicted in the short term, even considering an optimistic emissions scenario (Fig. 4–5). Indeed, a -95.6 % reduction of the potential range of this species is expected in the study area for the period 2041–2060 in the SSP126 projection, limiting the bioclimatic suitability for the Lanza's alpine salamander to 12.1 km^2. In the same period, applying the worst emissions scenario (SSP585), the predicted range contraction is -98.9 %, resulting in only 3 km^2 of suitable area. In the long term (2081–2100), a further range reduction is foreseen, leading to a climatically suitable area of 5.8 km^2 in the SSP126 scenario (-52.1 % from 2041–2060; -97.9 % from 2000–2020), while the bioclimatic suitability for *S. lanzai* is expected to run out from the study area in the SSP585 projection. Looking at the expected future trend of the predictors involved in the modelling procedure (Bio06, Bio09, Bio12 and Bio15), the bioclimatic suitability for the Lanza's alpine salamander in the study area will be largely compromised by increasing temperatures, together with a reduction in annual precipitations (predicted by the SSP585 scenario), and progressively higher values of precipitation seasonality (Fig. S2.3).

A declining trend is also highlighted by the IUCN distribution parameters calculated on the bioclimatic suitability model outputs (Fig. 6a–b). A -64.1 % EOO reduction is predicted in the short term in the SSP126 scenario (344 km^2), reaching the -95.1 % in the SSP585 condition (47 km^2). Then, the EOO is expected to further shrink (SSP126: -74.9 %; 241 km^2) in 2081–2100, even going to zero if the worst emissions scenario becomes a reality. Accordingly, the AOO shows a sudden decrease already in the 2041–2060 period while considering an optimistic emissions scenario (SSP126; -84.8 %; 100 km^2), even exacerbated in the long term (-95.7 %; 28 km^2). A -91.5 % AOO reduction (56 km^2) is expected in the short term according to the SSP585 projection, coming to a theoretical extinction of *S. lanzai* in 2081–2100.

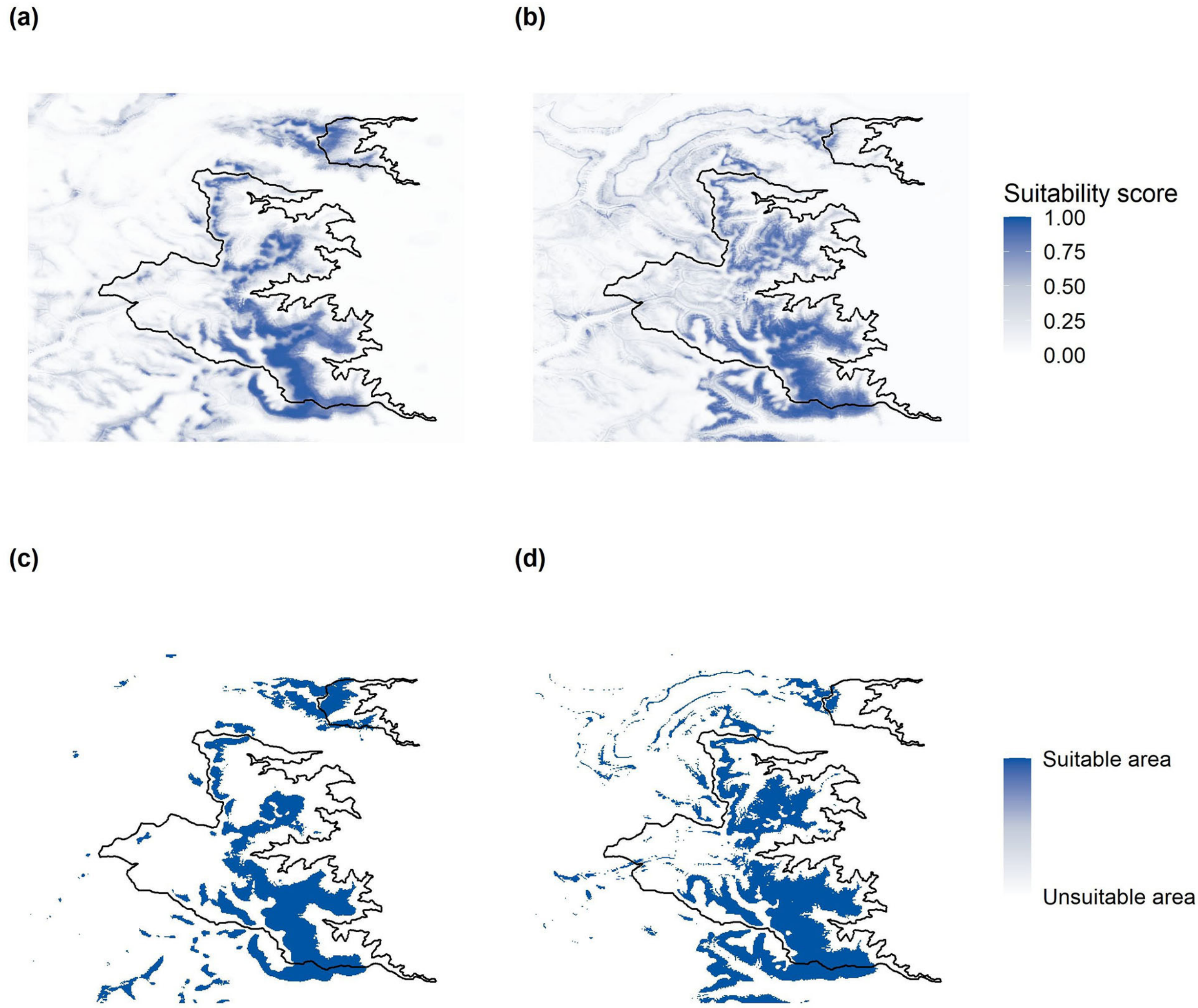

Figure 3. Current potential range of *S. lanzai* within the calibration area, as predicted by the environmental (a-c) and bioclimatic (b-d) suitability models. The suitable area is further highlighted in blue in the binary maps (c-d), according to the occurrence probability threshold that maximizes the TSS values. The black line identifies the perimeter of the study area considered in spatial analyses.

Following the predicted range contraction for the Lanza's alpine salamander and considering the current extent of protected areas (natural parks, natural reserves, and Natura 2000 sites), the climatically suitable area under formal environmental protection is expected to decrease in 2041–2060 (-10.2 %; 3.8 km^2) according to the SSP126 scenario, but then slightly increasing (+3.1 %; 2 km^2) towards the end of the century (Fig. 6c). Conversely, more than a half (56.7 %) of the remaining suitable area in 2041–2060 is forecasted to fall within protected areas in the SSP585 condition, although corresponding to an area of only 1.7 km^2. In this context, the Natura 2000 network is expected to fail in its contribution for *S. lanzai*'s protection, covering only the 12.4 % of the eligible area in 2041–2060 and the 3.4 % in 2081–2100 (SSP126), while no overlap between the species potential range and Special Areas of Conservation (SACs) is forecasted according to the SSP585 projections (Fig. 6c).

Together with a general reduction of the climatically suitable area for the Lanza's alpine salamander, future projections forecast an upward shift in the altitudinal range of the species (Fig. 6d). In particular, the mean predicted elevation is foreseen to shift of +324 m considering the SSP126 scenario in 2041–2060, increasing to +460 m in the SSP585 condition. Then, no significant changes in mean elevation are expected in 2081–2100 according to the SSP126 projection (-5 m from 2041–2060). Furthermore, predictions suggest that this upward shift will be more pronounced at the lower elevational limit for *S. lanzai*, where a +542 m shift is expected for 2041–2060 in the SSP126 scenario, compared with a change of only +4 m at the upper limit of the climatically suitable area for the species. This trend is even more apparent in the SSP585 projection, with a variation of +880 m and +4 m foreseen in the short term at the lower and the upper range limits respectively. In the long term, the lower elevational limit for the species is still expected to move upwards in the SSP126 condition (+141 m from 2041–2060), while the model forecasts no changes in the maximum elevation of the suitable area.

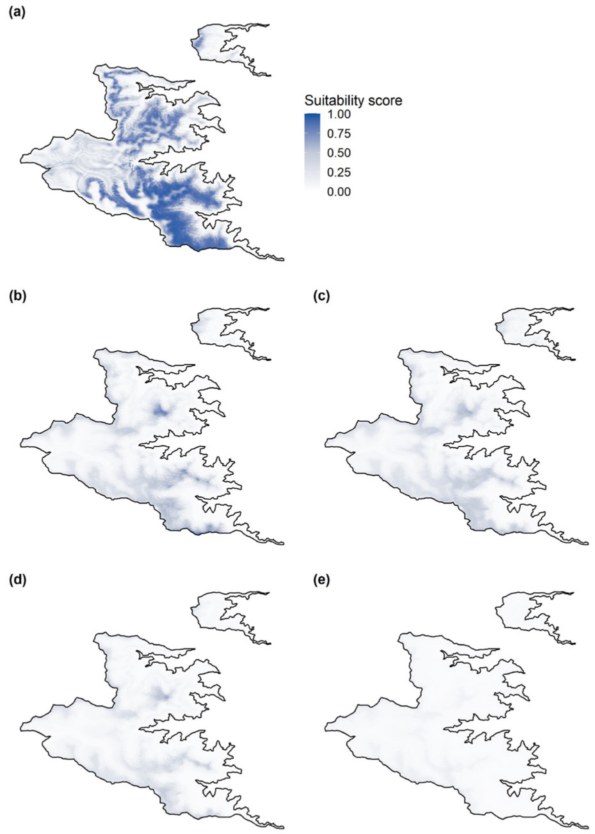

Figure 4. Future projections of the bioclimatic suitability for *S. lanzai* within the study area, according to two Shared Socio-economic Pathways (b, c: SSP126; d, e: SSP585) and two time periods (b, d: 2041–2060; c, e: 2081–2100). In a, the current bioclimatic suitability map is reported for comparison.

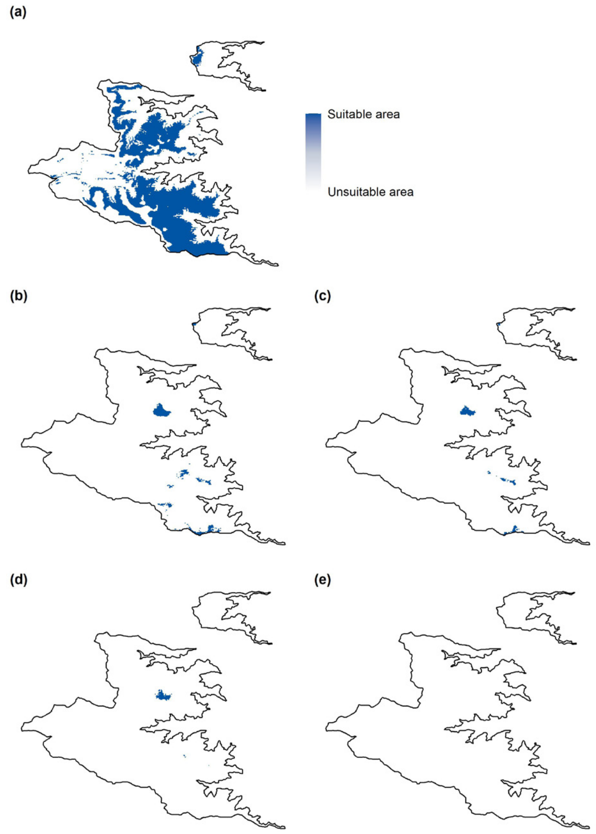

Figure 5. Future projections of the bioclimatic suitability for *S. lanzai* within the study area, according to two Shared Socio-economic Pathways (b, c: SSP126; d, e: SSP585) and two time periods (b, d: 2041–2060; c, e: 2081–2100). In this case, the predicted suitable area (in blue) is calculated according to the occurrence probability threshold that maximizes the TSS values. In a, the binary map concerning the current bioclimatic suitability is reported for comparison.

DISCUSSION

The SDM approach applied in this study provides a high-resolution statistical evaluation of the environmental and bioclimatic preferences of *S. lanzai* considering its whole distribution range. Although the effect of many fine-scale habitat features (e.g. micro-climatic conditions, availability of subterranean habitats, vegetation composition, etc.) and the species' thermoregulatory behaviour are not accounted for in the modelling procedure, the response of the Lanza's alpine salamander to the selected predictors is in accordance with the known ecological requirements of the species (Andreone, 2006), allowing for reliable projections in space and time. In particular, the overall propensity of this urodele for alpine grasslands and shrublands in relatively cold and humid (rainy) areas is confirmed, with cloud cover in summer positively affecting the occurrence probability of *S. lanzai*, highlighting a response to solar radiation similar to other mountain salamanders (e.g. Campbell Grant et al., 2018; Jacobsen et al., 2020).

Accordingly, the current environmental and bioclimatic suitability predicted by the ensemble models largely overlaps with the actual distribution range of the Lanza's alpine salamander, as confirmed by the new occurrence data collected in previously little-explored suitable areas during the targeted field surveys. However, models appear to overestimate the suitability for this amphibian in some portions of the calibration area, where observations are still lacking despite the specific field research carried out to validate model projections, leading to the exclusion of some environmentally and climatically suitable mountain sectors from the study area (likely falling outside the G_0 area, i.e. the actually occupied species range; Peterson et al., 2011; see Appendix S3).

In this context, although in previous studies on vertebrates the accuracy of climate-based SDMs was little improved after the addition of non-climatic predictors (Bucklin et al., 2015), the environmental suitability model shows a higher fitting with occurrence data than the bioclimatic suitability one (see AUC values), likely due to the major effect of June's solar radiation and July's NDVI in explaining *S. lanzai*'s distribution, exceeding the predictive capacity of most bioclimatic predictors. This results in a more conservative estimate in terms of extent of suitable area compared with bioclimatic model

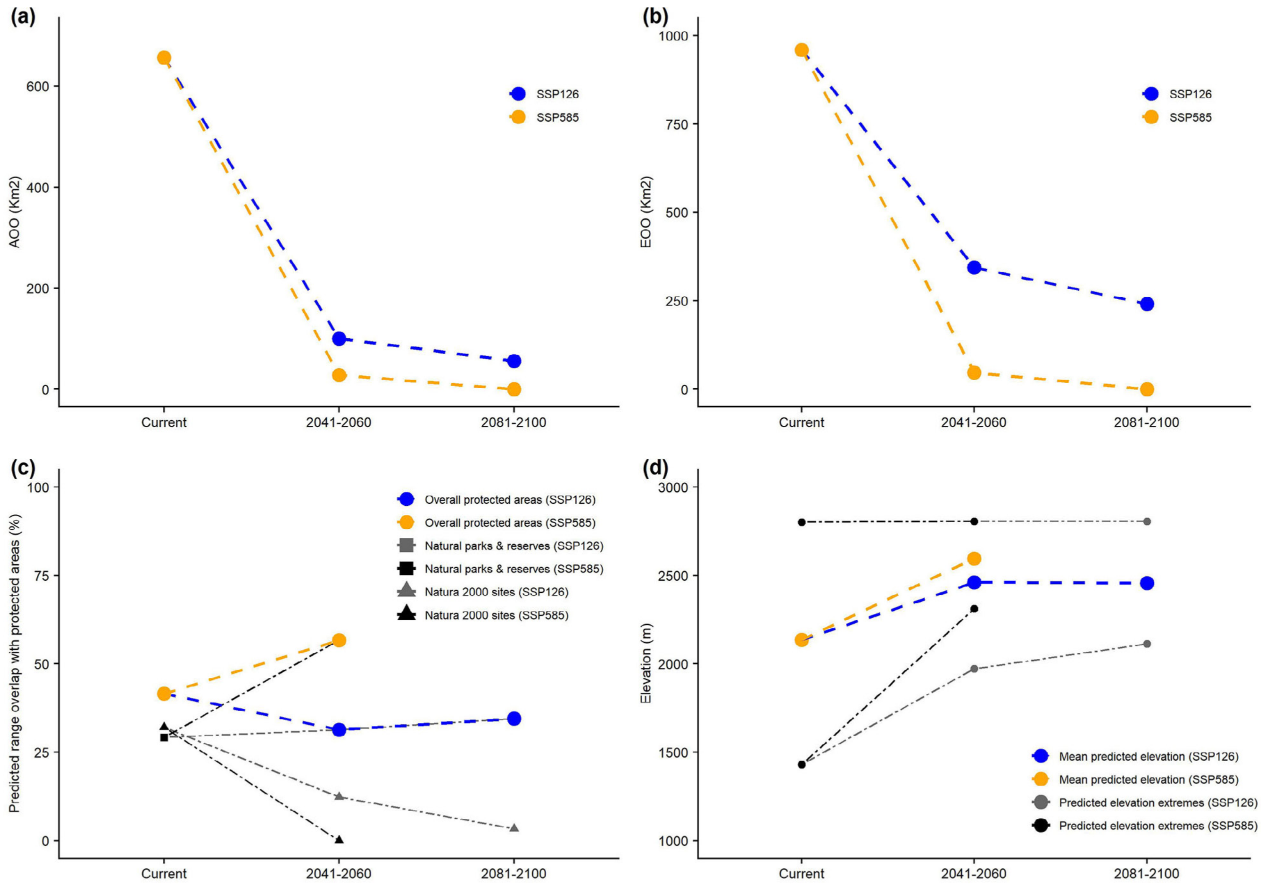

Figure 6. Plots reporting the current and predicted (2041–2060; 2081–2100) values concerning (a) the area of occurrence (AOO), (b) the extent of occurrence (EOO), (c) the range overlap with protected areas (natural park, natural reserves and Natura 2000 sites), and (d) the mean, minimum and maximum elevation of the distribution range for *S. lanzai* within the study area, according to the bioclimatic model outputs. Future projections are based on two Shared Socio-economic Pathways (SSP126 and SSP585).

outputs (226 km^2 vs. 274 km^2), to be used as reference to outline the current Lanza's alpine salamander's potential distribution, especially when planning short-term management and conservation projects or land use changes within the study area.

On the other hand, despite its lower accuracy, the bioclimatic suitability model represents an essential baseline to perform future predictions on *S. lanzai*'s suitable area, owing to the lack of future projections for all the parameters considered in the environmental suitability model. However, the relationship observed in the current scenario between environmental and bioclimatic suitability has to be taken into account when analysing future projections, especially considering that the environmentally suitable area may continue to represent a subset of the climatically suitable one through time (Kearney & Porter, 2009). Therefore, the dramatic range reduction predicted by the ensemble models in the next decades might be even worse, since the actual eligible area for Lanza's alpine salamanders in the future may cover only a portion of the remaining climatically suitable mountain sectors.

According to ensemble model forecasts, the suitable area for *S. lanzai* from a bioclimatic point of view will already decline significantly in the next 20–40 years, even considering an optimistic CO_2 emissions scenario, leading to a theoretical extinction of this species within the study area in 2100 in case the SSP585 condition will be actualised. As documented for other montane salamanders (e.g. Jacobsen et al., 2020; Lyons & Kozak, 2020), rising temperatures are one of the major factors in limiting the future bioclimatic suitability for the Lanza's alpine salamander, confirming global warming as an additional threat to the conservation of this critically endangered amphibian. Furthermore, changes in precipitation regimes within the study area are also expected to impact this species, especially if a reduced amount of rain will fall in few months throughout the year, thus increasing precipitation seasonality.

Together with an overall range contraction, ensemble models predict a considerable shift towards higher elevations of future suitable bioclimatic conditions for *S. lanzai*, as already predicted in central Alps for the alpine salamander *Salamandra atra* (Feldmeier et al., 2020), with pronounced changes expected in particular at the lower elevational limit for this species (as for instance observed by Campbell Grant et al., 2018). Given the rapidity and the size of the process, the complex mountain topography and the limited dispersal capacity of Lanza's alpine salamanders, many low-altitude populations may not be able to successfully track the predicted changes in bioclimatic suitability, possibly exacerbating the extinction risk for this amphibian in some sectors of the study area (Forero-Medina et al., 2011). Moreover, environmental suitability may not necessarily follow bioclimatic suitability shifts, resulting in an increasing proportion of actually unsuitable habitats towards mountain tops (e.g. rocky slopes, cliffs, etc.), in a context already constrained by the limited surface available (Elsen & Tingley, 2015), adding further limitations to the future upslope dispersal of salamanders.

The dramatic scenario highlighted by model predictions underlines the urgent need of up-to-date conservation and management strategies to ensure a successful mitigation of climate change effects on *S. lanzai*'s populations. First of all, the role of climatic variations in threatening the Lanza's alpine salamander has to be officialised by including this factor in the IUCN extinction risk assessment, a recognised tool to support decision-makers in setting conservation priorities, although no regulatory value is given to IUCN Red Lists. Indeed, the current assessment is based only on the presumed effect of the spreading lethal fungal pathogen *Batrachochytrium salamandrivorans* (*Bsal*), precautionarily listing *S. lanzai* as Critically Endangered (CR) in accordance with the criterion E (IUCN SSC Amphibian Specialist Group, 2022). Thanks to the estimation of the current and future extent of occurrence (EOO) and area of occupancy (AOO), this study provides useful data to incorporate also the criterion B (geographic range; IUCN Standards and Petitions Committee, 2022) in the Lanza's alpine salamander's assessment, although the expected changes in bioclimatic suitability cannot worsen the current threat category. However, a future range contraction and fragmentation have to be taken into account when considering the *Bsal*'s threat on *S. lanzai*, also considering the increased risk of contact with other upslope-dispersing amphibian species (Tiberti et al., 2021), including the congeneric European fire salamander *Salamandra salamandra* (Sillero, 2021).

A second important issue is that Lanza's alpine salamander populations should be adequately covered by protected areas, given its threat category and the strict protection regime required by the EU Directive 92/43/EEC, ensuring the application of effective and legally binding conservation measures. Today, less than 50 % of the environmentally suitable area for this urodele is included within natural parks and reserves or in Natura 2000 sites (with considerable gaps, especially in Italy), and this proportion seems to be maintained or even reduced in the future, according to the projected bioclimatic suitability. In this context, the EU Biodiversity Strategy for 2030 provides the opportunity for the designation of new protected areas in the western Alps, since Italy (as all EU member states) is asked to increase its proportion of legally protected land up to 30 % (i.e. +10 %; MITE, 2021) in the next few years. The current and future suitability maps provided in this study can guide decision-makers in identifying the most important sectors where *S. lanzai* needs protection, considering possible future range shifts due to climate change and candidate refuge areas (e.g. on the Cialancia massif and in the Po Valley), possibly including this species among the priorities considered to justify the enlargement or new designation of natural parks or Natura 2000 sites.

However, the establishment of new protected areas is not sufficient itself to increase the actual conservation status of the Lanza's alpine salamander. Active management, surveillance, and research are required to transform "paper parks" into effective biodiversity conservation authorities. For instance, all the known additional threats for *S. lanzai*'s conservation should be removed immediately, in order to prevent future detrimental combined effects with climate change. This is the case of roadkill mortality, severely affecting some Italian populations at low elevations along mountain roads, despite their overlap within Natura 2000 sites. As resulted by ensemble model predictions, low-altitude Lanza's alpine salamander populations are expected to be the most impacted by changes in bioclimatic suitability, thus requiring an urgent regulation addressed to minimise the passage of vehicles along roads intercepting suitable areas for salamanders, especially by night and in rainy or foggy days between May and September. Furthermore, since *S. lanzai* occurs in habitats that can be altered by overgrazing and livestock trampling, local grazing exclusion areas can be identified, as already implemented in France.

In conclusion, this study attempts to forecast a future reaction of the Lanza's alpine salamander to climate change, focusing in particular on space (i.e. possible range shifts following changes in bioclimatic suitability). However, this should be considered only as a first step towards a complete understanding of the process, since this species may track future climatic variations also by shifting its climatic niche along two other non-exclusive directions (Bellard et al., 2012): time (i.e. phenology) and self (i.e. physiology and behaviour). Thus, future bioclimatic suitability shifts might be buffered by phenological, physiological or behavioural adaptations, that should be considered as the next research target on this endemic urodele. In addition, continued monitoring is essential to follow through time the response of *S. lanzai*'s populations to changing climate and environment, confirming or rejecting the model predictions provided here, evaluating the effects of possible additional threatening factors (e.g. overgrazing, shrub encroachment, etc.) and hopefully testing the feasibility of possible climate change mitigation measures.

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