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Addressing conservation measures through fine-tuned species distribution models for an Italian endangered endemic anuran

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ABSTRACT

Climate and land cover changes are the two most important stressors causing the decline of amphibians' populations worldwide. Within the Mediterranean area, one of the global biodiversity hotspots, the endemic Italian yellow-bellied toad (*Bombina pachypus*) suffered the same fate, as the decreases and local extinctions proved over time. Since the need to preserve this Apennine endemic species is evident, we take advantage of a novel approach combining climate-based ecological niche models and post-modelling GIS techniques (i.e., the weighted overlay framework) to produce finer species distribution models for *B. pachypus*. In doing so, we coupled climate variables with topographic-, hydrologic-, and habitat-related predictors, sharpening the potential species' distribution at its whole range scale. Our findings show a latitudinal subdivision in predicted suitability: Central Apennines populations are expected to suffer more than the Northern ones, with considerable potential future losses of genetic diversity. On the contrary, Southern Apennines' suitability is predicted to remain stable over time, preserving the vast diversity. When assessing the coverage that protected areas offer to the locations of suitable habitats for *B. pachypus*, the protected sites of the Central Apennines result in slightly less suitable conservation areas than those in the Northern and Southern Apennines. The overall protected areas coverage is currently low (~20%) and predicted in the future to narrow towards medium suitability values, except in Southern Apennines, where an increase is inferred. In light of our spatially-explicit results, we suggest that a national-scale conservation strategy should consider different management options according to the sub-territories that our analyses highlighted. Our coupled "weighted modelling – spatialised genetic inference" approach permits us to support different conservation policies at all spatial scales, capitalising on relatively few input data. Also, in-depth spatial analyses should be performed to support effective protection strategies and management for the conservation stakeholders.

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1. Introduction

The latest IUCN reports indicate that 41% of all amphibian species are threatened by extinction (IUCN, 2021); due to this massive extinction trend and population decline, amphibian conservation has become a priority worldwide (Ficetola et al., 2015). Habitat loss and fragmentation, intensive agriculture, human-induced pollution, invasive species, diseases, and climate changes are the major factors that either act alone or in synergy, driving the amphibian decline (Hof et al., 2011; Bernabò et al., 2017; Scheele et al., 2019; Iannella et al., 2020). Besides, amphibian population response to threats varies geographically since the degree of exposure and the effect of each stressor is variable on a local, regional and continental scale (Grant et al., 2016; Grant et al., 2020). Changing climate can impact amphibian species distribution via a direct response to reduced habitat suitability or by shifting phenology and diminishing their fitness, impacting genetic diversity, modifying interactions among species or with pathogens (Miller et al., 2018; Abreu-Jardim et al., 2021) and references therein).

Within Europe, Italy has a high level of amphibian diversity, with nearly a third of endemism and a large proportion of threatened species (Temple and Cox, 2009; Rondinini et al., 2013; Sillero et al., 2014). Further, the Italian Peninsula is one of Europe's main southern glacial refugia, where pronounced diversification occurred and several distinct genetic lineages are present (Schmitt et al., 2021).

Over the past few years, considerable concern has grown on one of the most imperilled species endemic to the Italian peninsula, listed as "Endangered" in the IUCN Red List (Rondinini et al., 2013), the Apennine yellow-bellied toad *Bombina pachypus* (Bonaparte, 1838). This species occurs south of the Po Valley, through the Apennine chain, to the southern tip of Italy with a variable altitude range (from a few meters above sea level up to 1900 m a.s.l.) (Talarico et al., 2004; Sindaco et al., 2006). The current range of *B. pachypus* results from postglacial expansions from the refugial area in Southern Italy (Canestrelli et al., 2006). Previous studies have identified a hotspot area of genetic diversity for *B. pachypus* in the southernmost portion of its range, suggesting the potential conservation value of these populations (Canestrelli et al., 2013; Zampiglia et al., 2019). The Apennine yellow-bellied toad is strictly heliophilous, a typically prolonged breeder, and substantially philopatric (Lanza et al., 2007). The species is commonly found in ephemeral shallow and unshaded ponds, small temporary streams, and artificial water reservoirs where spawning and larval development occur (Mirabile et al., 2009; Romano et al., 2012). In the last decades, *B. pachypus* has experienced a sharp decline throughout the whole range, with huge decreases in populations size and local extinctions (Barbieri et al., 2004; Stagni et al., 2004; Mirabile et al., 2009; Canessa et al., 2013; Zampiglia et al., 2019; Vignoli et al., 2021; Bernabò et al., 2022). Loss or degradation of wetlands habitat, particularly temporary ponds and small human-made water bodies, drainage activities, climate change, and disease caused by the pathogenic fungus *Batrachochytrium dendrobatidis* have played a significant role (Stagni et al., 2004; D'Amen and Bombi, 2009; Canessa et al., 2013; Canestrelli et al., 2013). The Apennine yellow-bellied toad is listed in Appendix II of the Bern Convention and Annexes II and IV of the European Union Habitats Directive (92/43/EEC). According to Article 17 of the Habitats Directive, the latest assessment confirmed an unfavourable conservation status and a declining trend for this species (Stoch and Grignetti, 2021). *B. pachypus* could represent a key species for analysing the impact of land use and/or climate change on the spatial and temporal persistence of its populations; an in-depth knowledge picture of the possible scenarios permits to best define conservation priorities, thus answering questions on where targeting conservation efforts and on the effectiveness of the protected areas in preserving this species.

To date, conservation strategies for this species have been proposed on a national scale (Canestrelli et al., 2014). Several projects scattered along the Italian peninsula have mainly focused on management actions of breeding sites and reinforcement of the populations within the protected areas (Canessa et al., 2013; Salvidio et al., 2014; LIFE WetFlyAmphibia, 2019; Vignoli et al., 2021). These areas are one of the most prominent conservation tools playing an essential role in protecting biodiversity (Watson et al., 2014). However, their effectiveness currently and under future climate and land-cover changes remains to be evaluated (Vincent et al., 2019), especially for preserving amphibians and their species' genetic diversity (D'Amen et al., 2011; Nori et al., 2015; Abreu-Jardim et al., 2021). In this context, climate-based ecological niche models are increasingly incorporated in decision-making regarding land use and conservation, given their ability to predict species distribution under various climatic scenarios (Araújo et al., 2011). In Italy, few studies have evaluated the capability of the ensemble of nationally designated parks and Natura 2000 sites to preserve amphibians in current and future scenarios (D'Amen et al., 2010, 2011). These projections suggest that existing Italian protected areas are insufficient to conserve amphibian diversity.

Iannella and colleagues (2021a) recently proposed a 'couple-and-weigh' approach to refine the ecological niche models into a more informed spatial prediction, incorporating several environmental predictors in a post-modelling framework and thus increasing the predictive performance.

Our overarching aim is to identify the *B. pachypus*' future suitable areas and to infer whether the currently-established protected areas network contributes to protecting this species. We also test the effectiveness of the protected areas in preserving genetic diversity in future suitable zones. We gather a comprehensive occurrence localities' dataset and multiple environmental predictors (e.g., habitat types, topographic and hydrological-based variables) to infer fine-tuned species distribution models. We take advantage of the 'weighted' modelling approach to improve our understanding of *B. pachypus* ecology, distribution, and threats, thus targeting future research and setting conservation priorities in key areas.

2. Methods

2.1. Taxonomic status, occurrence data and study area

The taxonomic status of *Bombina pachypus* is currently controversial. Several authors consider *B. pachypus* a subspecies of

B. variegata (Linnaeus, 1758) based on molecular and phylogenetic data (Hofman et al., 2007; Zheng et al., 2009; Fijarczyk et al., 2011). Conversely, other authors have highlighted morphological and genetic differences between the yellow-bellied toads of Northern Italy and those of the Apennines, leading to recognising of a distinct species (Nascetti et al., 1983; Lanza and Vanni, 1991; Canestrelli et al., 2006). Accordingly, we considered *B. pachypus* a valid species.

We collected the Apennine yellow-bellied toad occurrence data from different sources: namely published literature (Ruffo and Stoch, 2005; Canestrelli et al., 2006; Mirabile et al., 2009; Fijarczyk et al., 2011; Mori and Giovani, 2012; Talarico et al., 2019), fieldwork data, and several herpetological databases that contained local georeferenced observations from 1982 to 2021 (DiBEST, University of Calabria; Calabrian section of the *Societas Herpetologica Italica*, and Dipartimento Ambiente Regione Calabria). Field surveys and sampling procedures were approved by the Italian Ministry of the Environment (permit numbers: PNM-2011-0002086 and PNM-2018-0012568). All these data were merged and filtered to be spatially and temporally consistent with the predictors used for the analyses (Sillero and Barbosa, 2020).

Considering the distribution of the target species occurring mainly in the Apennines (range digitised in Fig. 1b following Lanza et al. (2007)) and its possible accessible area *sensu* (Peterson and Soberón, 2012), we selected peninsular Italy as the study area. To supply better geographic references for the conservation-oriented final analyses, we took advantage of the Italian biogeographic provinces from Minelli et al. (2006) and Biondi et al. (2013), thus separating the outcomes in Northern, Central, and Southern Apennines areas (Fig. 1b).

2.2. Data integration and modelling workflow

For the present research, we applied a hierarchical modelling framework based on the ‘couple-and-weigh’ framework according to Iannella et al. (2021a), which permitted the sharpening of ecological niche models and the increase of predictive performance. We thus generated and managed the different environmental predictors in an ecological niche modelling and subsequent post-modelling weighting process (general workflow reported in Fig. 1a).

2.3. Environmental predictors and ecological niche modelling

To implement the weighted approach, we obtained environmental predictors from both international repositories and published technical data. Specifically, we downloaded the set of the nineteen bioclimatic variables from the Worldclim repository at 30 arc-second spatial resolution (ver. 2.1) for the current climatic conditions (Fick and Hijmans, 2017). To model future 2030, 2050, and 2070 scenarios, three different General Circulation Models (the BCC-CSM2-161 MR (Wu et al., 2019), the IPSL-CM6A-LR (Boucher et al., 2020) and the MIROC6 (Tatebe et al., 2019)) were downloaded to consider predictions’ uncertainties deriving from a single General Circulation Model-based approach (Stralberg et al., 2015). Also, two Shared Socio-economic Pathways, the SSP 3.70, and the SSP 5.85 were chosen to obtain separate future predictions. The former describes a future based on a difficult political path aiming at human impacts mitigation, while the latter depicts the “business as usual” scenario, in which development is based on fossil fuels and

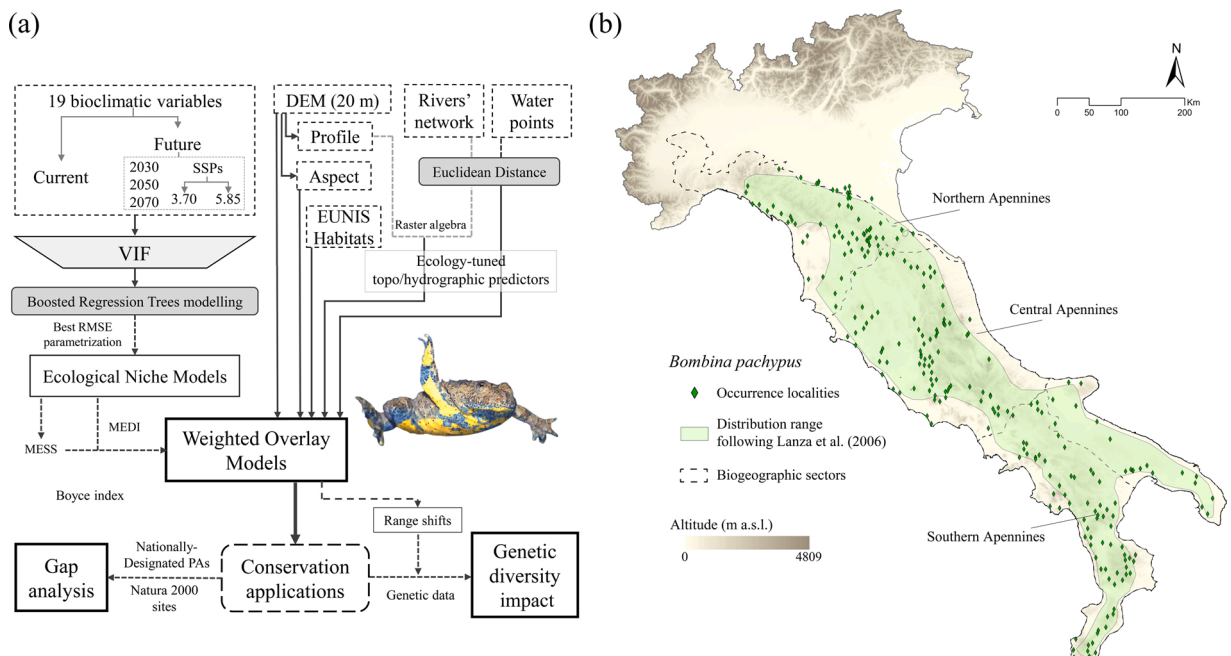


Fig. 1. (a) General workflow of the analyses, and (b) *Bombina pachypus* occurrence localities and distribution range.

natural resources depleted progressively (Fujimori et al., 2017; Kriegler et al., 2017; Riahi et al., 2017). To avoid correlation-related issues, we applied the Variance Inflation Factor algorithm (VIF, with threshold set = 10) of the ‘usdm’ R package (Naimi, 2015) to the set of bioclimatic variables. We then created 5000 pseudo-absence data using the ‘BIOMOD_FormatingData’ function of the ‘biomod2’ R package (Thuiller et al., 2016), and we assigned weights to both presences and pseudo-absences so that their respective sums equalled one another, following the ‘Weighted target-group background’ criteria from Cerasoli et al. (2017). Finally, we processed the selected variables with the presence – pseudo-absence data and through a Boosted Regression Trees modelling, implemented by the ‘gbm’ R package (Greenwell et al., 2019). To achieve the best modelling parametrisation, first, we built three matrices where different sub-settings were selected; then, we ran a number of models corresponding to all the possible combinations, finally choosing the parametrisation that results in the lowest root mean square error (RMSE) (Friedman, 2001; Cervellini et al., 2021). Specifically, *shrinkage* (overall range for the three matrices = 0.001 – 0.3), *interaction.depth* (1 – 7), *n.minobsinnode* (5 – 15), *bag.fraction* (0.65 – 1) and *n.trees* (10000 – 20000) parameters were iteratively changed while *train.fraction* (= 0.8) and the *cv.folds* (= 10) were maintained stable. We used the Boyce index to evaluate models’ performances (‘ENiRG’ R package (Canovas et al., 2016), *cv.sets* = 10), considering the presence – pseudo-absence approach (Boyce et al., 2002; Leroy et al., 2018).

To avoid extrapolation-related issues in projections to future climatic scenarios (i.e., the possible dissimilarity arising when models’ calibration and subsequent projection are performed with the same variables but reporting different ranges) and spatially assess it, we calculated the multivariate environmental surface similarity (MESS) for each General Circulation Model/SSP/year, through the ‘dismo’ R package (Hijmans and Elith, 2016). Then, we used these spatial data to implement the multivariate environmental dissimilarity index (MEDI) (Iannella et al., 2017). This index considers the extrapolation data deriving from the MESS maps, permitting to use GCM-derived projections into a final model, where each one is weighted based on its extrapolation degree. Therefore, we applied the MEDI maps to each SSP/year, merging the different General Circulation Models into one SSP/year, and buffering the corresponding extrapolation.

2.4. Weighted overlay environmental variables

We implemented into the ‘weighted’ post-modelling analyses a Digital Elevation Model at 20 m cell resolution, which we also employed to derive other two predictors: the aspect and the profile curvature of the whole study area. We chose the aspect (calculated through the ‘Aspect’ function in ArcGIS Pro 2.9) to infer the sun exposure of territories, considering the target species’ heliophilous nature (Lanza et al., 2007). Given the breeding habitat preference of *B. pachypus* for rock pools formed by slow-flowing waters in riverbanks (Lanza et al., 2007), we calculated the profile curvature (through the ‘Curvature’ function in ArcGIS Pro), which represents the curvature of the slope, to obtain a proxy for acceleration or deceleration of water flow (ESRI Inc., 2022), being thus more informative than the slope alone. We then multiplied the Profile curvature information with the Euclidean distance raster data calculated over the peninsular Italian surface running waters. We finally implemented into the weighted post-modelling this derivative variable, which depicts the areas where water flow is slow (or fast) together with the distance from the water body itself.

We gathered the source data of the aforementioned predictors from the geo-portal of the Italian Ministry of the Environment (<http://www.pcn.minambiente.it>). Similarly, we also calculated the Euclidean distance from springs, drinking troughs, fountains and ponds, retrieving these data for the whole study area from the official toponymy of the Italian Istituto Geografico Militare. Both the Euclidean distances were set at a maximum distance = 1200 m, based on dispersal capabilities known for *Bombina variegata* (Ptytycz and Bigaj, 1984; Cayuela et al., 2019).

To consider in the modelling process the Apennine yellow-bellied toad habitat preference, we downloaded the EUNIS (European Nature Information System) habitats’ raster map (at 100 m resolution) from the European Environment Agency website (<https://www.eea.europa.eu/data-and-maps/data/ecosystem-types-of-europe-1>). Since future spatial projections for these data are unavailable, we use the same maps for our current and future models’ projections, thus representing the ‘optimistic’ scenario of Iannella et al. (2021a), as urban areas are predicted to increase (Jiang and O’Neill, 2017). The main difficulty in predicting those changes is the spatialization of the variations in land use, as these predictions can be inferred mainly for agricultural contexts (Iannella et al., 2021b), based on dedicated databases (e.g., FAOSTAT database (FAO, 2017)). We finally assessed weighted models’ performance through the Boyce index (with the same parametrization of the paragraph above).

2.5. Weighted overlay post-modelling

First, we extracted occurrence-based raster information from the EUNIS habitats, elevation, and aspect predictors to implement the weighted post-modelling framework (‘Extract multi values to points’ tool in ArcGIS Pro). Second, we built frequency classes for each predictor, assigning the highest value (=10) to the most frequent one and reclassifying the predictors, based on their relative frequencies, to a 1-to-10 scale (‘Reclassify’ tool, ArcGIS Pro). This last process was also applied to the ecological niche models (current and future climate projections), which were reclassified to the same 1-to-10 scale based on their 0-to-1 scores. About the two water-related predictors (i.e., distance from rivers*profile curvature and distance from springs, drinking troughs, fountains and ponds), we reclassified their values by applying an inverse sigmoid function, considering the reported movement distance from water habitats with a range of 0–200 m (Ptytycz and Bigaj, 1984; Hartel, 2008). This distance interval was reclassified with the highest values, while the other distances were classified according to the inverse sigmoid trend, always following the 1-to-10 scale.

Lastly, we implemented all the predictors into the ‘Weighted overlay’ tool in ArcGIS Pro, setting the common scale for each at 1-to-10 and giving all the variables equal weights (20%), except for the two water-related ones, for which we assigned 10% of weight each. Even though we used high-precision datasets related to surface running waters and water-related toponyms, those may not completely

encompass all the different water environments, considering the national scale of our analyses. Thus, we preferred to slightly down-weight the two predictors preventively. The future ecological niche models were then implemented into the same process, and the occurrence localities falling within a 1200 m distance from the water-related sites were used to assess the future variations in suitability. This approach is helpful to depict changes in the species' occurrence sites that, more than a general trend, can support local-scale conservation measures.

Subsequently, we implemented the current and future binarised weighted predictions into a gap analysis. To do this, binarisation was obtained through the maximisation of the True Skill Statistics, TSSmax (Allouche et al., 2006) using the 'ecospat.max.tss' function of the 'ecospat' R package (Di Cola et al., 2017). We evaluated the protected areas' coverage for the Nationally Designated Areas (NDAs, such as National Parks and Reserves) and Natura 2000 sites (N2000, Sites of Community Importance (SCI) and Special Areas of Conservation (SAC). We also assessed the 'doubled' protection, that is the case where NDAs and N2000 sites overlap.

Finally, we used the current and future predicted binarised suitable areas together with the haplotype network extracted from Canestrelli et al. (2006); this allowed us to infer where the suitability changes would affect the target species' intraspecific diversity.

3. Results

After the data gathering and filtering, we obtained a final dataset with 1202 unique occurrences of *B. pachypus* (Fig. 1b) (from the initial 1414), which covers almost forty years (1982–2021).

Taking into account the VIF-based bioclimatic variables' selection, we considered the temperature isothermality (BIO3), the temperature seasonality (BIO4), the mean temperature of the wettest quarter (BIO8), the mean temperature of the driest quarter (BIO9), the precipitation of the wettest (BIO13) and driest (BIO14) month, the precipitation seasonality (BIO15) and the precipitation of the coldest quarter (BIO19) as modelling predictors. We found the overall lowest RSME for *interaction.depth* = 5, *shrinkage* = 0.001, *n.minobsinnode* = 10, and 12836 trees; these settings were used to calibrate and obtain the bioclimatic-based model (Supplementary material Figure A.1), which resulted in a Boyce index $B = 0.845$. The four most contributing variables were BIO9 (29.6%), BIO14 (13.7%), BIO3 (12.8%) and BIO8 (12.6%), with their marginal response curves reported in Fig. 2a. In addition, we found the two highest interactions between BIO9 and BIO8 and between BIO3 and BIO4 (Fig. 2b). About the topographic predictors used for the weighted process, we found *B. pachypus* mostly occurring in the 1000 – 1250 m a.s.l. interval and preferring East and North-East exposures (Supplementary material Figure A.2a and b, respectively), as resulted from the 'Extract multi values to points' process. Also, the occurrences' distance from water points did not exceed 50 m for the highest number (58.9%), followed by the 50–100 m interval with the 1.6% (Supplementary material Figure A.2c). Finally, the raster algebra between profile curvature and distance from rivers confirmed the preference of the target species for slow-moving (or still water segments of rivers), as the interval $-0.1 - +0.1$ (considering that 0 corresponds to a completely flat state) was the most frequent (43.8%) (Supplementary material Figure A.2d).

The outcomes of weighted modelling ($B = 0.915$) resulted in high predicted suitability covering the whole Apennine chain and the

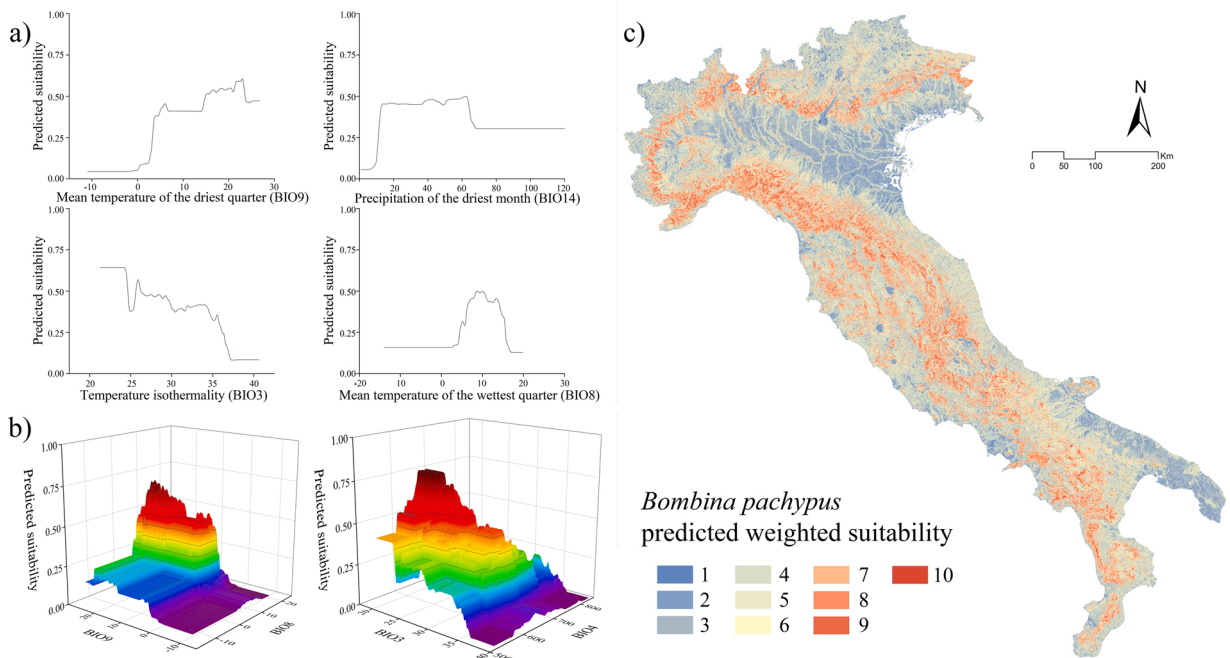


Fig. 2. (a) Marginal response curves of the four most contribution predictors and (b) their interaction; (c) *Bombina pachypus* predicted weighted suitability for the current climatic conditions.

Prealps and encompassing the Tuscan Apuan Alps, Metalliferous Hills and Maremma mountains, the Latial pre-Apennines and the Apulian Gargano (Fig. 2c). When binarising through the TSS-based threshold ($TSS_{max_threshold} = 0.41$; $TSS_{max} = 0.718$), we found the whole Apennine chain to be the most relevant and continuous sector, with some other patches partially or totally disconnected from the main thresholded area (Metalliferous Hills and Maremma mountains, Latial pre-Apennines and the Apulian Gargano).

When applying the current thresholded weighted model to the *B. pachypus* haplotype network (Fig. 3a), we observed vast predicted suitable areas for the haplotype 1 (h1) and its less wide-ranging related haplotypes (h2–5) (*sensu* Canestrelli et al., 2006). On the contrary, smaller and more clustered networks occur in the Calabrian region, well defined in a Northern (h6–8) and a Southern Calabrian one (h11–13) (Fig. 3a). The corresponding averaged future projections (Supplementary material Table A.1) showed a higher loss (and concurrent lower stability) in areas belonging to the ‘h1’ network if compared to the Calabrian ‘h6’ and ‘h11’ haplotypes, which behaved opposite (Fig. 3b). Also, we detailed the trends for all the occurring haplotypes, ordering by their geographic distribution (splitting ‘h1’ into two Northern and Southern sub-patches, see Fig. 3a and Canestrelli et al. (2006) and permitting us to arrange them into a North-to-South gradient. The ‘h4’ reported the highest loss rate, while ‘h8’ showed the lowest (Fig. 3c).

The North-to-South suitability trend led us to arrange the inferred future scenarios into the three Apennine biogeographic sectors, namely the Northern, Central, and Southern Apennines. We observed a general decrease in suitability within the whole occurrence localities’ dataset, especially for what concerns the Central Apennines (Fig. 4). Specifically, suitability decreases from 2030 to the 2070 projections (left to right points, for each sector), with the SSP_3.70 points group showing higher suitability with respect to the one of the SSP_5.85 (high to low points, for each sector) (Fig. 4a). The suitability loss during subsequent future decades-different SSPs combinations is also observable in the radar graph (Fig. 4b), where Southern Apennines emerge for their higher scores.

Finally, we found different protection assets in nationally- or internationally- designated protected areas, as observed from the gap analysis (Fig. 5). Currently, NDAs and N2000 sites protect almost the same percentage (~ 20%) of the territories predicted as moderately suitable for *B. pachypus*, except for the Northern Apennines, where higher suitability is protected if compared to the two other sectors (Fig. 5a). Also, N2000 sites in the Central Apennines cover areas with higher suitability compared to the NDAs (Fig. 5b). When analysing the future trends, the percentage of both protected areas’ categories increases (~ 27%), even though shifting towards lower suitability in the Northern and Central Apennines (Fig. 5a and b). On the contrary, the Southern Apennines maintain the suitability range increasing the protection to more than 30% (Fig. 5c). If comparing these trends with the current and average future suitability occurring in each biogeographic sector, conformity among the distribution of the overall suitable areas and the respective proportion of protection can be noted. Indeed, a slight shift towards the protection of mid-suitable areas is observed for the Northern and Southern Apennines, with a more pronounced trend reported for the former.

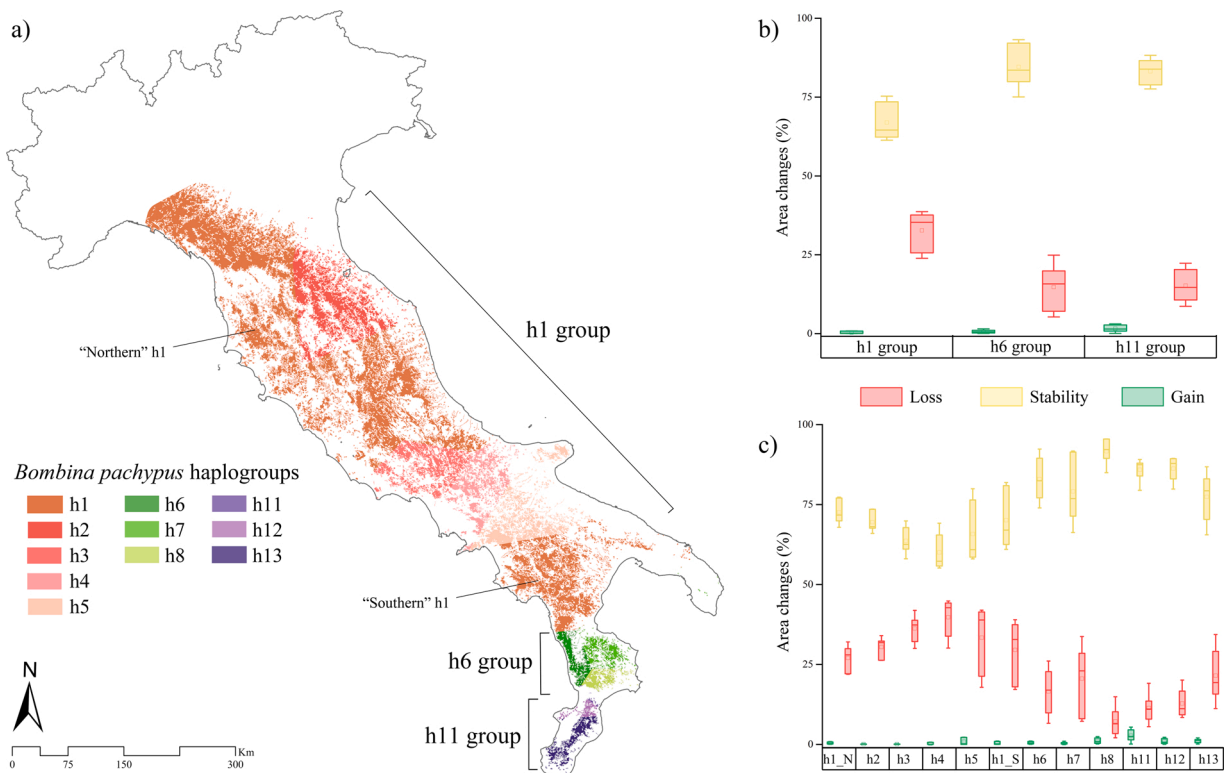


Fig. 3. (a) *Bombina pachypus* haplotype network inferred over binarised weighted suitability for current conditions and (b) the corresponding average future changes for haplogroups and (c) haplotypes.

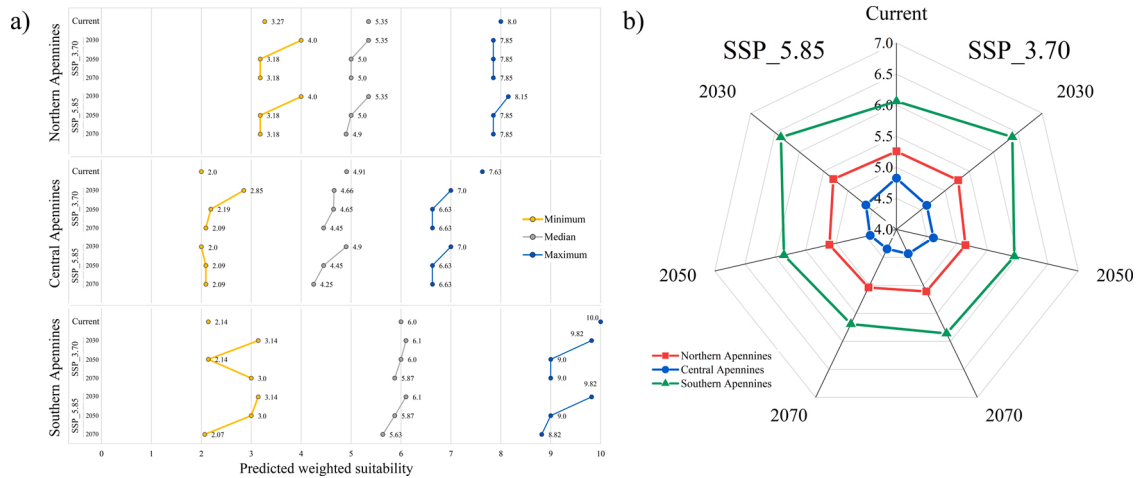


Fig. 4. Changes in *Bombina pachypus*' suitability of territories around occurrence localities over years_SSP, within each biogeographic sector, measured at their (a) minimum, median, maximum and (b) average values.

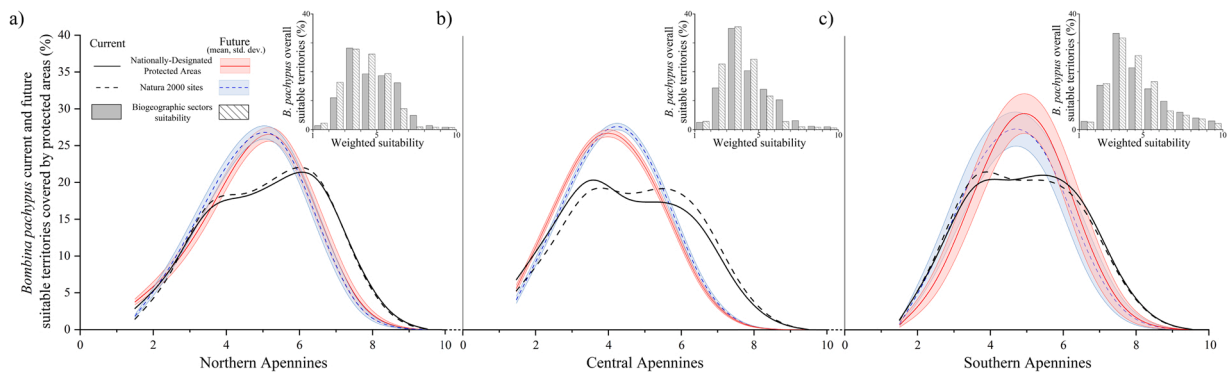


Fig. 5. Predicted suitability distribution within the currently-established protected areas' network in the (a) Northern, (b) Central, and (c) Southern Apennines for current (black lines) and averaged future (coloured lines) conditions and overall predicted suitability (upper right panel).

4. Discussion

Understanding the ecological requirements of the Apennine yellow-bellied toad *Bombina pachypus* at its whole-distribution scale poses the essential basis for an effective conservation strategy. Our study achieved two different but converging modelling outcomes aiming at this goal.

From the ecological niche modelling process, which resulted in high-performance scores, we first obtained sound evidence of the climatic requirements of the target species. Our findings highlight the importance of climate-related covariates for *B. pachypus* phenology. The most contributing variables identify a positive response in spring/summer and especially in summer periods.

Specifically, the temperature must be high during summers (as indicated by BIO9), and precipitations occur even at a minimal amount, being thus enough to support a comprehensive suitability range (as observable by the BIO14 curve). This latter trend indicates a need for year-long climatic stability, also reinforced by the inverse relation reported for the isothermality curve (BIO3), in which a decrease in suitability is related to the decrease in the annual temperature range. Moreover, the 'stability need' is confirmed as the interaction peaks are observed in a mid-range of spring/autumn temperatures and temperature seasonality.

In the analysis of the bioclimatic niche, all the identified trends tie-in with the ecology of *B. pachypus*, mainly focusing on its reproductive biology (Guarino et al., 1998). Other studies on *B. pachypus* and co-generic species indicate sensitivity to summer covariates and support our finding that Apennine yellow-bellied toad is more sensitive to variation in temperature seasonality during the breeding season. It has been demonstrated that temperature and precipitation are crucial determinants of post-metamorphic survival and reproduction and that varying weather conditions in the spring result in strong variation in the survival of immature yellow-bellied toads (Cayuella et al., 2014, 2016). Moreover, rainwater fluctuations and extreme drought events are expected to impact the fitness and recruitment of *B. pachypus*, because this species reproduces mainly in temporary water bodies (Barbieri et al., 2004; Mirabile et al., 2009).

The positive response of *B. pachypus* to warmer summer may support a suggested hypothesis related to the immune function of

those amphibians preferring warmer temperatures; namely, higher extreme temperatures could indirectly benefit populations by increasing the ability to counteract infections caused by pathogens such as chytrid fungus (Miller et al., 2018; Sauer et al., 2018).

Considering limited dispersal abilities, projections for future climate scenarios showed a reduction in suitable areas for *B. pachypus* (considered a lineage of *B. variegata*) that may compromise its persistence (Boyer et al., 2021). As recommended by these authors, here we try to make more accurate predictions on local variations driven by future climate changes. The outcomes of the weighted overlay analyses give other interesting insights. The suitable patches are more restricted to specific areas (and sub-areas) with respect to those predicted by the ecological niche models alone, as confirmed by the higher discrimination power we found for the weighted model. Moreover, the inferred distribution is consistent with the known range reported from the Italian Fauna (Lanza et al., 2007).

In detail, the suitable Prealpine areas are predicted only by the weighted model based on predictors other than the climate-based ecological niche model, with this latter reporting a sharp suitability decrease in the passage between the Ligurian Apennines and the Maritime Alps. The characteristic Apennine distribution of *B. pachypus* may thus be related to climate constrain, considering that the other environmental factors occurring in the Prealps are favourable to the species. Likewise, the vast climatically suitable areas in the Calabrian peninsula are narrowed to sharper 'weighted' patches, mainly located along the Catena Costiera and in the Pollino, Sila and Aspromonte massifs, where the complex topography of the region might mitigate the impact of climate. Also, our overall findings are congruent with those of other authors on future climate suitability (Zampiglia et al., 2019).

Concerning the future weighted scenarios, we found a general suitability decrease in the proximity of the water environments where the species occurs. The descending trend goes along the increasing years (i.e., from 2030 to 2070), with the SSP_5.85 being the worst case. Specifically, Central Apennines yielded the highest suitability losses, while Southern Apennines were less affected by the decrease, and Northern Apennines were placed in a mid-position. This trend seems particularly important given that some populations could decline faster than others due to changes in water availability during the breeding season.

The same tendency is also confirmed at the whole study area scale, considering the outcomes of the haplotype network analyses based on the binarised models. The higher stability is reported for the two Calabrian (Southern) haplogroups ('h6' and 'h11' sensu Canestrelli et al. (2006)), while the 'h1' (representing the Northern and Central Apennines) loses on average the ~ 30% of predicted suitable future areas. When taking advantage of the sub-networks, an evident bimodal North-to-South trend along the Apennine peninsula emerges from the analyses. Northern patches lose more than 25% of their territories, Central ones almost reach 50% of losses, while Southern patches generally maintain their entirety. Moreover, Southern (Calabrian) haplogroups show little gains, a trend which could balance possible losses.

Coupling these species' diversity patterns with the protected sites' safeguard capabilities raises several concerns from a conservation perspective. Aside from the fact that the protected areas' network currently covers a low percentage of suitable areas, future inferences predict a complex suitability scenario. Moreover, it is also evident that the protected areas are located accordingly to where the suitability occurs (i.e., the proportion of areas covered by protected sites goes along with the general suitability distribution), thus not offering comparable protection to the crucial, highly suitable habitat patches. A similar pattern also emerged in D'Amen et al. (2011), which considered the total amphibian diversity. Indeed, across the territories covered by NDAs and N2000, our weighted projections report a non-uniform trend in which protected areas of the Northern and Central Apennines behave differently compared to the Southern ones. This trend suggests the need to apply different local approaches to the specific territorial context if one wants to preserve *B. pachypus*, at least considering the three Apennines biogeographic sectors. For instance, in Central Apennines, conservation efforts should focus on specific sub-areas where reproductive sites should be monitored and preserved, as drastically-reduced habitat suitability is predicted. Thus, pond constructions and the restoration of degraded wetlands aiming to reintroduce or reinforce populations might be successful in granting their long-term survival and in promoting their resilience. Even though these measures could sound simple to address, it must be noted that the core of the Central Apennines' NDAs (i.e., the Sibillini, Gran Sasso-Laga, Majella, Sirente-Velino, Simbruini and Abruzzo-Lazio-Molise National Parks) shows high suitability in fragmented patches or only towards their borders. This last issue may slow or hinder the management at the small scale, as protected areas should then negotiate protection plans with local stakeholders (e.g., municipalities), which could have different regulations based on the territorial context they occur within (e.g., provinces, regions, etc.). Also, if considering the fragmentation occurring in highly suitable patches, the effort of protected areas should be greater, especially in terms of enhancing ecological connectivity and limiting road mortality. On the contrary, in the Northern Apennines, protection measures could be addressed in wider areas, considering the ecological connections among populations as a result of a lower fragmentation of highly suitable areas.

Concerning the Southern part of the Apennines, the models herein demonstrate that this sector represents a crucial area where conservation is (and will be) the most important in preserving genetic diversity. This area is considered a unique refugium and harbours populations genetically more diverse and differentiated (resulting from allopatric speciation and postglacial admixture) than northern populations (Canestrelli et al., 2006, 2012; Schmitt et al., 2021). The representatives of all the haplotypes of the target species occur in the Southern Apennines, with the Calabrian peninsula hosting populations of *B. pachypus* with the highest overall diversity (Canestrelli et al., 2006; Zampiglia et al., 2019). Therefore, we agree with Zampiglia and colleagues (2019) on targeting intra-specific hotspots of genetic diversity as conservation priorities for the endangered Apennine yellow-bellied toad. Considering the contiguity of the northern Calabrian patches (Pollino, Catena Costiera and Sila massifs) and the isolation of the southern one (Aspromonte chain), a 'mixed' approach of both small-scale conservation actions and ecological connectivity inferred at a larger scale should support *B. pachypus* populations' management. In addition, recent research dealing with the distribution and ecological requirements of *B. pachypus* in the southernmost part of Italy also showed that Catena Costiera and NDAs covering the Pollino, Serre and Aspromonte territories are the main statistically-significant hotspots, although these NDAs protect far less than the Natura 2000 sites (Bernabò et al., 2022).

Our findings provide a basic instrument for directing effective conservation practices in the long-term management and also supply

a framework to be adapted to inform conservation actions for other threatened taxa, considering the worldwide alarming changes in geographic ranges currently observed for many vertebrates (Cerasoli et al., 2019; Iannella et al., 2021a; Liang et al., 2021). Future works should delve further into the complexities of the observed responses (e.g. possibility of moving through the landscape or the narrow-scale protected areas' coverage), as well as more detailed studies should be conducted at the local scale for optimising conservation planning (given that local contexts may include geographic, biotic and abiotic factors that differ in importance). Also, one should consider the limitations of our predictions, as they do not include diseases or pathogens (e.g. chytridiomycosis) which affect the target species, or stochastic events, such as flash floods or localized extreme droughts. Lastly, we strongly recommend a national recovery plan for *B. pachypus*, indicating a comprehensive and effective protection strategy for the conservation stakeholders.

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CRedit authorship contribution statement

IB and MI conceived the ideas and carried out the design of the paper. IB, VC, ES and MI carried out data collection. MI analysed the data with input from IB and MB. IB and MI led the writing of the manuscript, supported by MB. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02302](https://doi.org/10.1016/j.gecco.2022.e02302).

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