

ARTICLE

Animal Ecology

Unraveling the drivers of amphibian community distribution at a lowland–mountain interface: A joint modeling approach

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Abstract

Understanding how environmental and biotic processes jointly shape species distributions and community composition is a central goal in ecology. Although species distribution models (SDMs) have become essential tools for quantifying environmental drivers of occurrence, their single-species framework limits inference about interspecific relationships and community-level patterns. Joint species distribution models (JSDMs) are multispecies distribution models which explicitly acknowledge the multivariate nature of communities, modeling all species at once and considering their interactions. They can be the basis for further community analysis, such as bioregionalization, supplying further insights to ecologically understand and manage a study area. Despite their potential, these methodologies are rarely applied, especially regarding terrestrial vertebrates and small geographical scale. Here, we integrated JSDMs with a data-driven bioregionalization approach (regions of common profile, RCPs), to explore the determinants of amphibian assemblages and their spatial turnover at a local scale. We applied this framework to 10 amphibian taxa in Oltrepò Pavese (northern Italy), a heterogeneous landscape at the interface between the Po Plain and the Northern Apennines. We specifically investigated the environmental drivers of species distribution and the residual co-occurrence patterns, relying on the framework Hierarchical Modelling of Species Communities (HMSC). Then, the predicted joint occurrences were used to bioregionalize the study area. Species showed differential effects of environmental covariates. Significant co-occurrence patterns were highlighted, mostly attributable to factors not explicitly included in the model, such as the type of breeding site. We identified three RCPs, with distinct amphibian assemblages: a lowland region, dominated by farmland adapted species; a transitional one which lies in the lower Apennine and hosts widespread species, quite tolerant but probably not enough for the over-exploited Po plain; and a mountain region with microtherm and forest amphibians. Alarming, the

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first two RCPs are dominated by the alien marsh frog *Pelophylax ridibundus*, which reached the area in 2005. The work supported the applicability of the HMSC framework to amphibians and the definition of RCPs at a local scale. This integrated approach offers a method to assess community structure and turnover across environmental gradients, an essential step for understanding and conserving biodiversity in rapidly changing landscapes.

KEYWORDS

amphibia, biological invasion, bioregionalization, community ecology, conservation, ecological modeling, hierarchical modeling of species communities (HMSC), joint species distribution modeling, species distribution modeling (SDM)

INTRODUCTION

One of the main aims of ecology is to understand the factors affecting species distribution and abundance (Smith, 1968). This issue, historically approached in an anecdotal and descriptive manner, is now being answered using quantitative methods. Several approaches have been applied in order to identify these factors and quantify their importance. Among them, the ever-developing family of species distribution models (SDMs) has emerged some decades ago and has established itself as the most widely used (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). Besides individuating drivers of distribution, SDMs allow predicting such distributions, calculating species occurrence probability or “suitability” in each unit of the study area (Elith & Leathwick, 2009). As a result, SDMs have immediately emerged as a major tool used for a wide range of tasks, from basic ecology to conservation and management, for example, studying niches characteristics; understanding ecological requirements of endangered species; figuring out biogeographical pattern; evaluating invasiveness of introduced species; predicting effects of climate and human-mediated changes on populations; planning protected area and reintroductions (Araújo et al., 2019; Franklin, 2023; Hirzel & Le Lay, 2008; Lissovsky et al., 2021; Peterson, 2006; Srivastava et al., 2019).

One of the intrinsic constraints of the early SDM approaches was that, irrespective of the proposed algorithm, they could model one species at a time, thus limiting the possible community-level analysis to the assemblages of several single-species models (Guisan & Rahbek, 2011). Such an additive approach to multispecies SDMs inevitably results simplistic, as it ignores information about species interactions in modeling distribution, thus implicitly assuming that the process leading to the observed spatial pattern has not been directly affected by any biotic factor (the “B” in the BAM diagram, Biotic Abiotic Movements; Sillero, 2011; Soberón, 2007), or, alternatively, that abiotic factors might capture these

processes, serving as a proxy. To overcome this issue, true multispecies approaches have been subsequently proposed and defined as joint species distribution models (JSDMs), which give the opportunity to explicitly consider interactions between species, and to borrow information from one species and another, improving modeling of their niches (Ovaskainen et al., 2017; Ovaskainen & Soininen, 2011; Warton et al., 2015). This kind of multispecies models, embedded in the framework hierarchical modeling of species communities (HMSC), can explore species-specific responses to environmental variables and simultaneously account for interactions across *taxa* and allows answering several ecological questions at once (Cranston et al., 2024; Ovaskainen et al., 2017; Soanes et al., 2024). Further, HMSC can greatly improve typically community-level analysis such as “bioregionalization” (Foster et al., 2013; Ovaskainen & Abrego, 2020), which can be of great ecological and conservation interest (Foster et al., 2013; Hill et al., 2017). Bioregionalization corresponds to the identification of discrete ecologically meaningful units within a given area, each characterized by unique and defined species assemblages (Lomolino et al., 2016), and inevitably requires a community-level approach. One of the most direct ways to define such geographical entities relies on the concept of regions of common profile (RCPs): an RCP is a portion of the environmental space where the vector of predicted species’ probabilities of being found is (relatively) constant and distinct from other regions (Foster et al., 2013). By providing vector of occurrence probability estimated by HMSC, it should be possible to obtain more realistic RCPs compared to those derived by separately estimating probability for each species. The use of interrelated species occurrence probabilities, in turn, may improve knowledge of the drivers of local beta-diversity, with a significant impact on conservation management.

Although the HMSC framework is increasingly being applied (e.g., Bonfim et al., 2024; Custer et al., 2024; König et al., 2024; Seoane et al., 2023) and the same is

occurring for the concept of data-driven bioregionalization (Hill et al., 2017; Woolley et al., 2020), to our knowledge, the combination of these tools has never been attempted, at least concerning land environments and vertebrate *taxa*, although a couple of case studies involving demersal fish and butterflies have been presented (Hill et al., 2020; Ovaskainen et al., 2017). Further, bioregionalization based on terrestrial vertebrates has been applied to macroecological studies at the global level (Falaschi et al., 2023; Ficetola et al., 2021; Holt et al., 2013), but never at local scale, where it could directly support management and conservation actions by providing a more complete picture than the widespread umbrella species concept (Roberge & Angelstam, 2004; Wang et al., 2021).

To start filling the gap, the present work has the purpose of demonstrating the potential for the combination of HMSC and RCP approaches, giving support to the use of these emerging tools to enhance both ecological knowledge and conservation strategies, thus expanding the data-driven bioregionalization concept to the small geographic scale and showing its applicability to vertebrate communities with a limited number of species. The study system was set up on amphibian populations in the Oltrepò Pavese district, a small region in northern Italy between the Po Valley and the Northern Apennines. This allows us to deepen the ecological knowledge of an interesting and heterogeneous area, answering specific ecological questions.

Amphibians, as well known, are the most threatened class of vertebrates at the world level (IUCN, 2024). Their decline, despite encouraging cases of both successful conservation actions (Moor et al., 2022) and innovative solutions (Waddle et al., 2024), is not stopping globally (Luedtke et al., 2023). In the last global evaluation, climate change has been recognized as the main driver of status deterioration and northern Italy as a hotspot of threat, especially for the potential spread of diseases (Luedtke et al., 2023). Italy is characterized by high levels of endemism across *taxa* (Amori & Castiglia, 2018; Massa & Fontana, 2020; Selvi et al., 2023), and amphibians are not an exception (Sillero et al., 2014). Besides conservation issues, amphibians also provide a good study case to test both HMSC and RCP approaches, since their need for water to succeed in reproduction constrains species to co-occur and share reproductive sites, naturally leading to species assemblages (López-de Sancha et al., 2025). Nonetheless, HMSC has been applied to amphibians in just two very different cases, both oriented towards assessing species interaction, in one case in congener salamanders (Gould & Peterman, 2024) and in the other in wetland birds and fishes (Kačergytė et al., 2023).

The Oltrepò Pavese (Lombardy, northern Italy) is a relatively small area (about 1097 km²) set at the interface between the Po Plain and the Northern Apennine, thus encompassing two ecoregions with very different characteristics: Central (Po) Plain Subsection and Toscana and Emilia-Romagna Apennine Subsection, belonging to the Po Plain Province and Apennine Province, respectively (Blasi et al., 2014, 2018). Amphibian communities and their drivers have been studied in the Po Plain (Ficetola & de Bernardi, 2004; Ildos & Ancona, 1994) as well as in the Apennines (Biancolini et al., 2024; Costa et al., 2025; Romano et al., 2012), although in their northern section studies focused on single species (Canessa et al., 2013; Mangiacotti et al., 2025) or environments (Manenti & Pennati, 2016). However, there is a lack of research investigating the distribution and ecological preferences of amphibians at the interface between these two different but closely connected regions, giving us the opportunity to apply the RCP framework on a relatively small scale.

Combining HMSC and RCP approaches, in this study we want to specifically address three different issues: (1) identifying climatic and land cover factors driving amphibian assemblage distribution; (2) shedding light on the role, if any, of species interactions in shaping co-occurrence patterns; (3) defining RCPs, comparing them with recognized ecoregions (Blasi et al., 2018) and with special attention to the location and species composition of a possible transition zone. A side point of interest is to assess the distribution and role in species assemblages of a harmful alien species, the marsh frog *Pelophylax ridibundus* (Pille et al., 2024).

MATERIALS AND METHODS

Study region

We conducted our study in Oltrepò Pavese (Lombardy, northern Italy; Figure 1). Due to its position which embraces plain and mountain areas, the Oltrepò is characterized by a great heterogeneity of environments and notable gradients both of habitat and of climate. The altitudinal gradient ranges from about 50 m above sea level to 1754 m (Mt. Lesima), along a north–south axis. The climate regime is temperate/mesothermal according to the Koppen classification (Bordoni et al., 2019), with differences within the area mainly related to altitude. The main land cover types are arable land and impervious surfaces in the lowland with an increasing proportion of broadleaved forest, paired with a fragmented distribution of permanent grasslands, rising in altitude; the lower hills



FIGURE 1 Location and map of the study area (Oltrepò Pavese). The target species included in the analysis are shown on the left and bottom edges. From the top left: *Triturus carnifex*, *Lissotriton vulgaris*, *Rana dalmatina*, *Pelophylax ridibundus*, *Ichthyosaura alpestris*, *Bufo bufo*, *Hyla intermedia*, *Bufotes viridis*, *Rana italica*, *Salamandra salamandra*. Photo credits: Martino Flego and Alice Funk.

are characterized by a high proportion of vineyards, constituting a cultural landscape typical of the study area (Brambilla & Ronchi, 2020).

Target species

We aimed to map as best as possible the distribution of all amphibian species found in Oltrepò Pavese, building the basis for subsequent modeling. Species consist of six Caudata—*Triturus carnifex*, *Lissotriton vulgaris*, *Ichthyosaura alpestris*, *Salamandra salamandra*, *Salamandrina perspicillata*, and *Speleomantes strinatii*—and seven autochthonous Anura—*Hyla intermedia*, *Bufo bufo*, *Bufotes viridis*, *Rana italica*, *Rana dalmatina*, *Rana temporaria*, and *Pelophylax synkl. esculentus* (Bernini et al., 2004). The alien marsh frog *P. ridibundus* is also present and abundant in the study area. This species has been introduced in northwestern Italy in 1941, spread in past decades, and is expected to continue to do so

(Falaschi et al., 2018; Lanza, 1962), with high risks for native amphibians, mainly related to predation and genetic pollution (Bruni et al., 2020; Pille et al., 2023, 2024). In the study area, the species first appeared in 2005 and rapidly spread across the plain portions and the bottom of the valley of the main river (Razzetti et al., 2010). Among other species, several are endemic or subendemic to the Italian peninsula at the species (i.e., *T. carnifex*, *S. perspicillata*, *S. strinatii*, *H. intermedia*, and *R. italica*) or subspecies level (i.e., *I. alpestris apuana* and *B. viridis balearicus*) (Sindaco & Razzetti, 2021).

Occurrence data and fieldwork

An intensive campaign was conducted in 2024 to collect amphibian presence points, covering all species in the study area and their entire breeding season (February–July), for a total of 73 survey days. Field activities can be divided into four main tasks, aimed at

conducting adequate species-specific surveys to maximize detection probability: (1) Monitoring of wetlands known by previous projects. Most of the wetland locations were obtained from the pond census conducted by Pellitteri-Rosa et al. (2010) which individuated 194 wetlands in Oltrepò Pavese. This number was supplemented by ad hoc surveys in the months preceding the field activity, reaching a total of 252 sites. Each site was surveyed one to three times between February and July. (2) Searching for new breeding sites, by walking trails, especially in areas with fewer already known wetlands. We walked a total of 274 km, taking the GPS location of observed amphibians and breeding sites (including potential ones). (3) Monitoring of species with notable calling activity: *H. intermedia*, *B. viridis*, and *Pelophylax* sp. for which call survey is a suggested census technique (Stoch & Genovesi, 2016). We drove a total of 435 km by night at low speed, stopping near wetlands or ditches, or whenever we heard calling, for listening session of at least 10 min. (4) Targeted surveys on *R. italica*, searching for adults and tadpoles along streams. This endemic species is strictly related to running waters where individuals spend most of the year (Lanza et al., 2007), given that adults are elusive and primarily nocturnal, searching for tadpoles is an advantageous methodology (Stoch & Genovesi, 2016).

The occurrence data were made unique within pixels of 500×500 m. We choose this grain as a compromise between high-resolution species distribution modeling, avoiding duplicates in the case of larger wetlands, reducing spatial autocorrelation and allowing sufficient aggregation between points of occurrence of different species. Such a scale was used in other studies which applied species distribution modeling to amphibians (e.g., Gerick et al., 2014; Préau et al., 2018). We included occurrence points beyond administrative limits of Oltrepò Pavese for a maximum of 5 km.

Environmental predictors

We aimed to individuate drivers of amphibian distribution and community assemblage both among climatic and land cover variables, since both can represent key factors and using their combination has been shown to outperform climate-only models when applying species distribution modeling to amphibians (Seaborn et al., 2021).

Climatic data were obtained from the free software ClimateEU v4.63 (Marchi et al., 2020), which allows downscaling climatic variables at the requested scale, providing coordinates and altitude as input. We provided as locations the centroids of a 500×500 m grid built on

the study area and derived monthly average temperature and rainfall for the decade 2011–2020. We used the output to calculate three bioclimatic variables: bio01 (mean annual temperature), bio04 (temperature seasonality = $SD \times 100$), bio12 (cumulative annual precipitation) as indicated in the WorldClim database (Fick & Hijmans, 2017). In this way, we obtained a measure of the two principal climatic factors with a dispersion index for temperature. However, all these bioclimatic variables turned out to be highly correlated with each other, so we kept exclusively bio01 as predictor ($r_{bio04} = 0.91$, $r_{bio12} = -0.89$).

We derived land cover variables from the Land Cover Map 2022 produced by ISPRA, the Italian Institute for Environmental Protection and Research (<https://groupware.sinanet.isprambiente.it/uso-copertura-e-consumo-di-suolo>, accessed on 7 November 2024). This map is obtained by integrating data from Copernicus Land Monitoring Services (<https://land.copernicus.eu/en>, accessed on 7 November 2024) and the National Map of Land Consumption produced by ISPRA itself (Luti et al., 2021). The result is a raster layer with high spatial (10×10 m) and thematic (13 land cover classes) resolution. We discarded the land cover classes underrepresented in the study area, reducing them to 5: broadleaf forests, coniferous forests, periodic herbaceous (crops), permanent herbaceous, shrubs; we split the latter category in natural shrubs and vineyards, intersecting the map with the ISPRA Land Use Map (<https://groupware.sinanet.isprambiente.it/uso-copertura-e-consumo-di-suolo>, accessed on 7 November 2024), resulting in a total of six categories. Percentage of coverage within the 500×500 -m pixels was calculated for each class.

Besides climate and land cover, landscape characteristics and heterogeneity can have an important role in predicting species occurrence and have recently claimed to be included in species distribution modeling (Riva et al., 2024). To address this need, we included a measure of thematic diversity in our predictors by calculating Shannon's index on land cover proportions (McGarigal & Marks, 1995; Shannon, 1948).

Statistical analysis

All the analyses were run in R environment (v. 4.4.0) (R Core Team, 2024). We managed and prepared spatial data using the package *terra* (Hijmans, 2020). We modeled species distribution and responses to environmental variables in the framework HMSC (Ovaskainen et al., 2017). In practice, Bayesian JSDMs were fitted using the R package *Hmsc* (Tikhonov et al., 2020). We modeled amphibians' presence/absence using a probit distribution. The presence matrix was obtained from the 500×500 m pixels with at least one presence point,

considered as the sample units (rows), while the species constituted the columns. Before running the models, we checked for multicollinearity among variables, and we had to remove a land cover class (periodic herbaceous); after this removal, all remaining variables had a variance inflation factor below 5 (Menard, 2002). So, we ultimately included in the models as fixed effects the coverage of five land cover classes, the Shannon index and the mean annual temperature (bio01). Each covariate was scaled and included as a second-degree polynomial, to consider possible quadratic effects and species optima at intermediate levels.

HMSC enables modeling of species associations by measuring the covariance structure of model residuals. Species associations are estimated in the random effect part of the HMSC model (Ovaskainen & Abrego, 2020). The random effect can be spatially explicit to control for the spatial structure of the residuals (Ovaskainen et al., 2016). We preliminary ran a set of models, using the default prior distributions and sampling the posterior distribution with four short Markov Chain Monte Carlo (MCMC) chains (samples = 250, thinning = 10, burn-in = 1250) to assess the importance of random effects inclusion in the HMSC models and whether fixed effects provide more information than the mere spatial structure of the data: ENV (only fixed effects), ENVRL (fixed effects and sample unit-level random effect), ENVSPAT (fixed effects and spatial random effect), and SPAT (only spatial random effect, without fixed effects). We compared these models using three metrics: root mean square error (RMSE) between predicted and observed values, AUC (area under a relative operating characteristic curve; Pearce & Ferrier, 2000), and Tjur R^2 (Tjur, 2009).

We chose the best model and sampled the posterior distribution with four MCMC chains, each running for 375,000 iterations, removing the first 125,000 as burn-in and with a thinning interval of 1000. Thus, we kept 250 samples per chain, for a total of 1000.

We analyzed the drivers of species distribution and community assemblage in four steps: (1) partitioning of the explained variation to identify the most important factors among covariate fixed effects and random effect; (2) individuating responses to the environmental variables by exploring β parameter estimates and response curves; we described the distribution of each β calculating maximum a posteriori (MAP) probability estimate and highest density interval (HDI) with a credible interval of 0.89 (Kruschke, 2015), using the package bayestestR (Makowski et al., 2019); (3) computing residual species associations to individuate patterns of co-occurrence; and (4) identifying RCPs (Foster et al., 2013), clustering species based on their predicted occurrence

probabilities (Ovaskainen & Abrego, 2020). For the latter purpose, we chose the number of clusters using the Elbow method as implemented in the R packages *factoextra* and *Nbclust* (Charrad et al., 2014; Kassambara & Mundt, 2016).

RESULTS

Occurrence data

We collected 840 amphibian occurrences in total. We removed the duplicates within 500×500 m pixels. Discarding species with less than 15 presences at this resolution (*S. perspicillata*, *S. strinatii*, *R. temporaria*, *P. synkl. esculentus*), this resulted in a set of 275 pixels with a minimum of one amphibian species and a maximum of six.

Notably, we did not find any populations that could be definitively attributed to native *Pelophylax*, while many sites with non-native taxa were identified, even outside the historical range of the native species (Bernini et al., 2004). From now on, we will refer to the non-native group as *Pelophylax* sp., considering the intricate taxonomy of the genus, even in the study area (Bellati et al., 2023). The most common taxon is by far the alien *Pelophylax*, widespread in almost the entire study area, while the less commonly encountered is *S. salamandra* (Table 1).

Model evaluation

The preliminary analysis of whether to include a random part in the model and whether to consider it spatially structured showed clear indications. The inclusion of a random effect increased the performance of the model by all metrics, especially by Tjur R^2 (Table 2). There were

TABLE 1 Numbers of occurrences per species in 500×500 m pixels.

Species	Occurrence cells (N)
<i>Pelophylax</i> sp.	179
<i>Lissotriton vulgaris</i>	47
<i>Bufo viridis</i>	42
<i>Rana dalmatina</i>	37
<i>Triturus carnifex</i>	35
<i>Ichthyosaura alpestris</i>	27
<i>Hyla intermedia</i>	27
<i>Rana italica</i>	24
<i>Bufo bufo</i>	18
<i>Salamandra salamandra</i>	16

TABLE 2 Comparison between the four models: only fixed effects (ENV), fixed effects and sample unit-level random effect (ENVRL), fixed effects and spatial random effect (ENVSPAT), and only spatial random effect without fixed effects (SPAT).

Model	AUC	Tjur R^2	RMSE
ENV	0.87	0.27	0.27
ENVRL	0.95	0.41	0.22
ENVSPAT	0.9	0.39	0.23
SPAT	0.88	0.15	0.29

Note: The reported metrics are area under the curve (AUC), Tjur's R^2 (Tjur R^2), and root mean square error (RMSE).

not remarkable differences between considering the random effect spatially structured or not. We therefore chose not to consider it structured, keeping the model simpler and reducing the computational effort.

The final model, run with longer MCMC chains, showed good convergence. The effective sizes were 1033 ± 10 (mean $\pm$ SE), while the potential scale reduction factors for the β parameters were all close to 1 and under the threshold of 1.1 (Gelman & Rubin, 1992).

Response to environmental variables and residual associations

Partitioning of the variation showed that most of it was explained by land cover, while the climatic variable contributes 4%–45%, and the random effect of the sample unit was the less important driver for most species, excluding *T. carnifex* and *L. vulgaris* (Figure 2; Appendix S1: Table S1).

Looking at the single variables' importance, contributions varied considerably among species, with bio01 and vineyard the only ones above 5% for all of them (Appendix S1: Table S2). Regarding the effects and their signs, below we report the ones of variables with at least one of the two β (first- or second-degree term) that have 89% credibility interval, computed as the HDI of posterior distributions, that did not contain zero.

Bio01 had a positive effect on the probability of occurrence of *H. intermedia* and *B. viridis*, while *I. alpestris* was more likely to occur at low temperatures; *T. carnifex*, *Pelophylax* sp., *R. dalmatina*, and *R. italica* presented a negative second-degree term, indicating a temperature optimum, in the case of the last two species shifted towards lower values while centered on higher values for *Pelophylax*. Vineyards positively affected *T. carnifex*, *L. vulgaris*, *R. dalmatina*, and *B. bufo*; in the case of *Pelophylax* sp., the positive sign of first-degree β was associated with the negative of second-degree one, with a drop of occurrence beyond high values; finally, *B. viridis* and *H. intermedia* lose probability of occurrence beyond

fairly low coverage values. Permanent herbaceous had negative second-degree β for *L. vulgaris*, *B. bufo*, and *R. italica* (in the latter case associated with a positive first-degree one); for *Pelophylax* sp., β s were negative and positive for the first and second degrees, respectively. Broadleaf forests had a positive effect on *R. dalmatina*, *I. alpestris*, *R. italica*, and *S. salamandra*. Needle-leaved forests had a linear positive effect on *S. salamandra*, *R. dalmatina*, and *Pelophylax* sp., for the latter two associated with a negative quadratic one; *H. intermedia* is instead negatively affected. Shrubs only affected *R. italica*, with a negative second-degree term. Finally, *B. viridis* was negatively influenced by Shannon index, with a slightly positive second-degree term. All the response curves and the beta estimates are available in Appendix S1: Figure S1 and Table S3; some of the most notable ones, concerning bio01, vineyards, and broadleaf forests, are provided below as examples to highlight the differential responses of species (Figure 3).

Analyses of residual associations among species revealed a positive co-occurrence pattern, with a support level above 0.95 credibility, among *R. dalmatina*, *T. carnifex*, *L. vulgaris*, and *I. alpestris*. These species were all negatively associated with *R. italica* (Figure 4).

Regions of common profile

According to the Elbow method, the optimal number of clusters was three, thus leading to the definition of three RCPs where the probability of occurrence of the species varied sharply. Region 1 was dominated by *Pelophylax* sp., with a significant presence of *H. intermedia* and *B. viridis*; in Region 2, the most abundant species did not change but the probability of presence of *R. dalmatina*, *B. bufo*, and the two newts *T.s carnifex* and *L. vulgaris* increased. Finally, in Region 3, *I. alpestris*, *R. italica*, and *S. salamandra* became the most common species (Table 3). Observing their projection in space, Region 1 corresponded to the plain part of the study area, Region 2 was distributed mainly in the hilly belt, while Region 3 was purely Apennine (Figure 5).

Evaluating the correspondence with the ecoregions of Italy (Blasi et al., 2018), we see that Region 1 belongs to the Po Plain Province while Regions 2 and 3 belong to the Apennine Province.

DISCUSSION

In this work, we combined the use of joint species distribution modeling (in the framework HMSC) and bioregionalization at local scale (RCP) to (1) analyze the factors

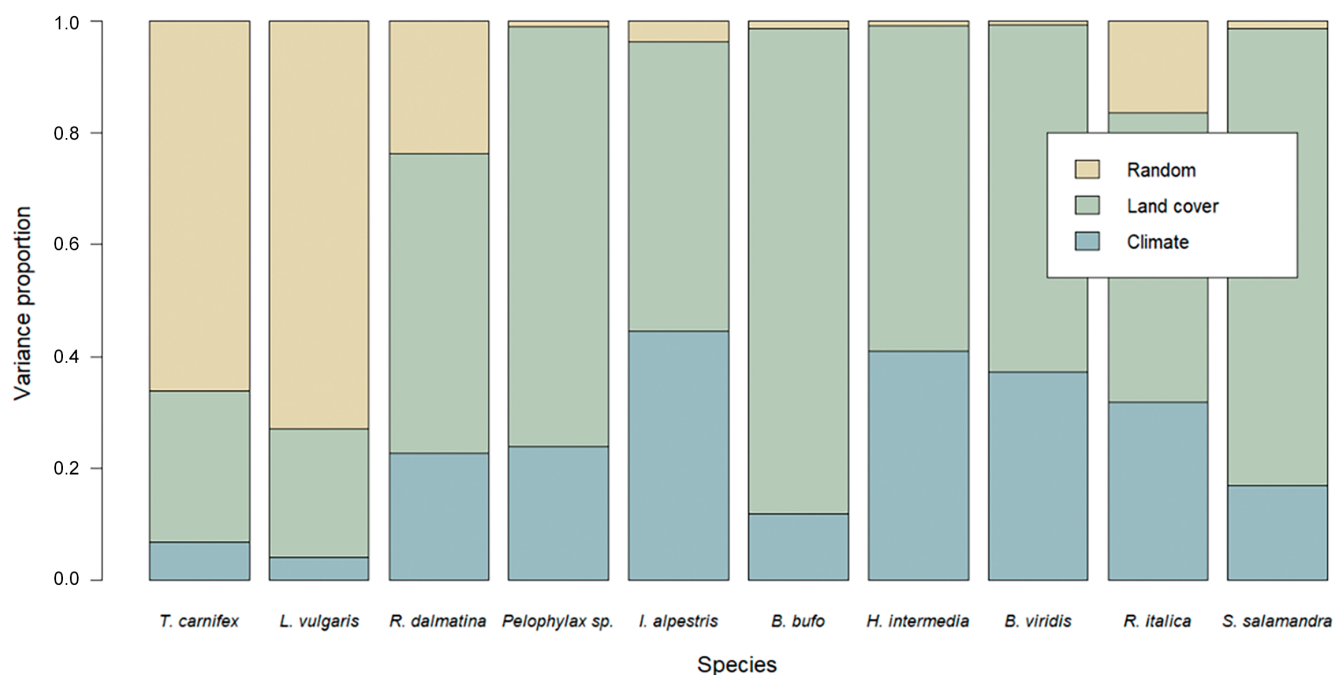


FIGURE 2 Proportion of explained variation among the climatic variable (mean annual temperature), land cover, and sample unit random effect.

affecting amphibian distribution at the interface between a lowland and a mountain environment in northern Italy, (2) shed light on residual co-occurrence patterns, and (3) identify species assemblages and their turnover based on the predicted occurrence probabilities. The combination of the two approaches gave ecologically meaningful results, both considering the single-species and community perspective. HMSC simultaneously pinpointed the main distribution drivers of the studied species, disentangling the effects of climatic and land cover variables. The species that exhibit a higher importance of climate are the most stenothermic ones. *I. alpestris* is the only real cold-adapted species considered in this study (Chiocchio et al., 2017), and climate accounts for 45% of its explained variation. Although occurring at relatively low altitudes, *R. italica* is mainly related to hilly and mountainous areas (Sindaco et al., 2006), and the values of variation explained by climate is 31%. On the other hand, *H. intermedia* and *B. viridis*, two lowland and thermophilic species (Derakhshan & Nokhbatolfoghahai, 2015; Dufresnes et al., 2018), show values of 41% and 37%, respectively, highlighting the importance of temperature for both cold- and warm-adapted species. Although the above proportions should be interpreted with caution, also due to the different number of variables considered in the two blocks (one climatic and five land cover), they are consistent with the species ecology (Lanza et al., 2007). The alpine newt shows strong responses to climate, with probability

of occurrence falling to zero beyond species-specific temperature thresholds. On the contrary, species with a broader altitudinal range showed no significant response or bell-shaped response curves, such as in the case of *R. dalmatina* (Lanza et al., 2007).

Land cover also showed particularly important effects (more than 50% variation explained), especially for species requiring specific habitats. Notably, the positive effect of broadleaf forests on *I. alpestris*, *R. italica*, *R. dalmatina*, and *S. salamandra* confirms the strong relation of the latter three species with woodlands; also, *I. alpestris*, even if adaptable to many different types of breeding sites, is related to forest habitat, especially for its terrestrial phase (Denoël & Ficetola, 2008; Naumov et al., 2020). The positive effect of vineyards on *T. carnifex*, *L. vulgaris*, *R. dalmatina*, and *B. bufo* is probably due to the availability of artificial ponds related to viticultural activities. These ponds are usually stable and quite deep (more than 1 m), representing good breeding sites for the above-mentioned species. On the other hand, the pond features and the scarcity of other types of wetlands, such as canals or temporary pools, in this kind of agriculture, explain the negative effects on *B. viridis* and *H. intermedia* (Ebisuno & Gentili, 2002; Landler et al., 2023). This represents another evidence of the role of agricultural-related water sites in shaping amphibian communities and their distribution, as found in other contexts and in the Apennine itself (e.g., Caballero-Díaz et al., 2022; Costa et al., 2025; Romano et al., 2023).

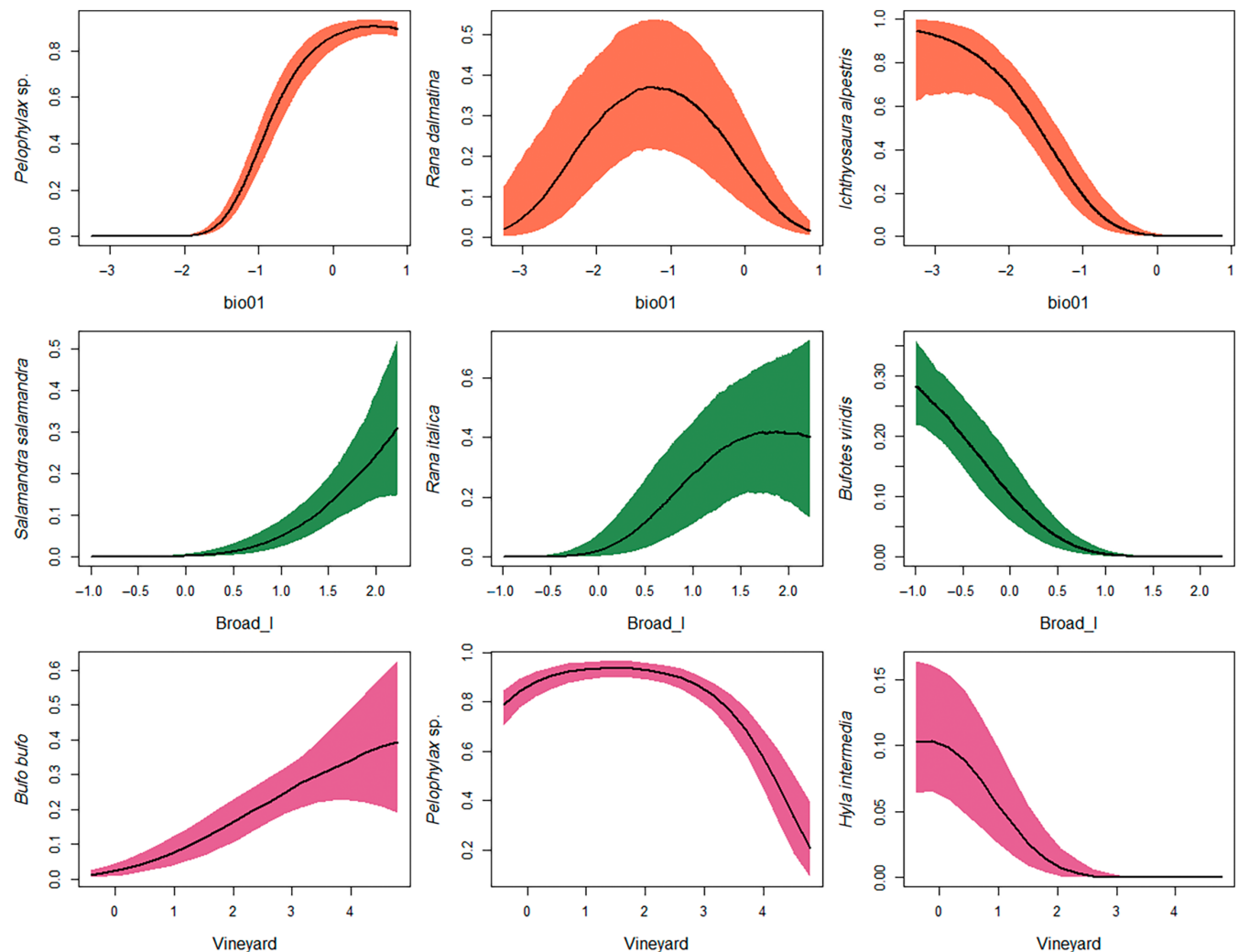


FIGURE 3 Curves representing the predicted responses to variable variations. The values on the y-axis are occurrence probabilities of the labeled species; the credibility intervals are delimited by the first and third quartiles. Here, some of the most notable curves are reported to highlight species-specific responses to environmental gradients. All curves are available in Appendix S1: Figure S1.

All the above results showed that a multispecies approach provides the same outcomes in terms of climatic and habitat selection as the classical single-species approach. However, the multispecies approach has an added value: the inclusion of a random effect, which allows estimating species residual associations, increasing model performance. On the other hand, caution should be exercised when interpreting residual associations: When statistically supported, they may indicate real interactions among species, as well as variations attributable to factors not controlled by the model (Ovaskainen & Abrego, 2020). In our case, the positive association among *L. vulgaris*, *T. carnifex*, *I. alpestris*, and *R. dalmatina* is not thought to reflect species direct interactions, but rather the shared microhabitat preferences not included in the fixed part of the model; indeed, these species are the most strictly *pond-breeder* ones (Lanza et al.,

2007). The capture of breeding site type preferences by the random part of the model is confirmed by the negative association among the latter species and *R. italica*, which spawns exclusively in lotic environments. Patterns based on the type of breeding habitat, captured by latent variables, have also recently been identified by Costa et al. (2025) in the Apennine region. The fact that the model did not capture real biotic interaction but rather unmodeled microhabitat type could be seen as a disadvantage; however, its ability to account for features that are difficult to explicitly include in a SDM (e.g., mapping the number of ponds for each cell of the study area would be almost impossible) could be a further strength of the HMSC approach.

Based on the presence probabilities derived from the multispecies model, we could identify three RCPs, geographically corresponding to three distinct zones: an

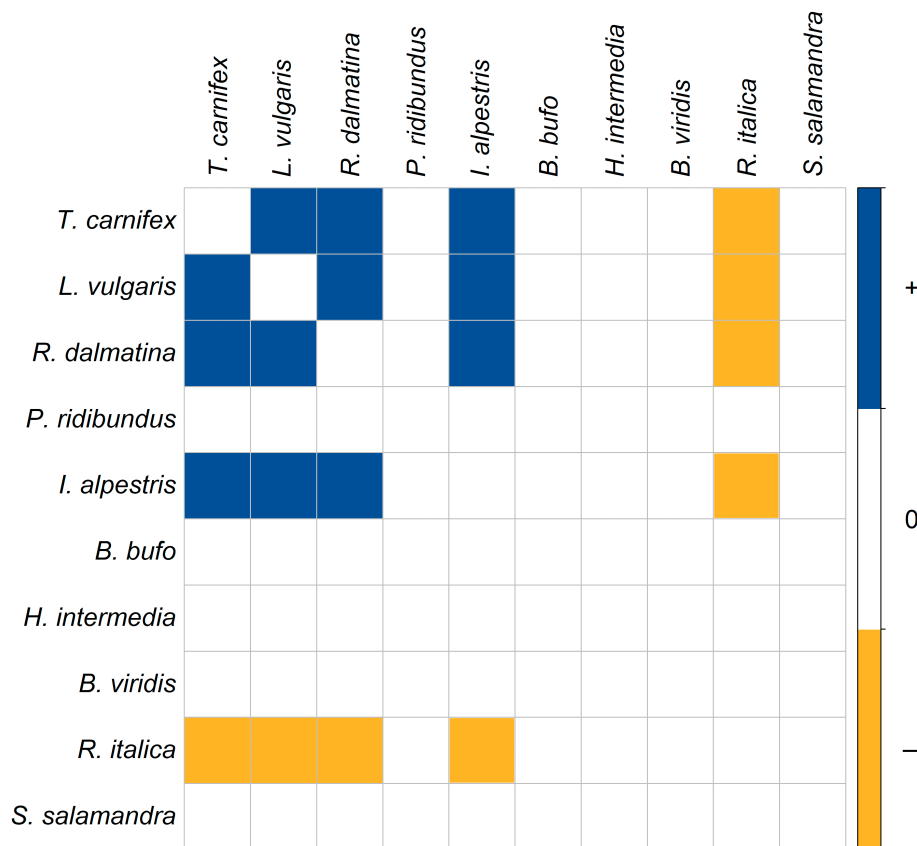


FIGURE 4 Residual species associations. Associations estimated to be positive with a probability of at least 0.95 are shown in yellow, those estimated to be negative in blue. In white, associations were not statistically supported.

TABLE 3 Five most common amphibian species in each region of common profile (RCP), with the probability of occurrence (prob.).

No.	Region 1		Region 2		Region 3	
	Species	Prob.	Species	Prob.	Species	Prob.
1	<i>Pelophylax</i> sp.	0.83	<i>Pelophylax</i> sp.	0.72	<i>Ichthyosaura alpestris</i>	0.34
2	<i>Bufo viridis</i>	0.36	<i>Rana dalmatina</i>	0.2	<i>Salamandra salamandra</i>	0.26
3	<i>Hyla intermedia</i>	0.19	<i>Bufo bufo</i>	0.12	<i>Rana italica</i>	0.21
4	<i>Rana dalmatina</i>	0.01	<i>Lissotriton vulgaris</i>	0.11	<i>Rana dalmatina</i>	0.18
5	<i>Bufo bufo</i>	0.01	<i>Triturus carnifex</i>	0.08	<i>Bufo bufo</i>	0.11

Apennine one, a lowland one, and a hilly and transitional one; the latter acting somewhat as an interface between the former two, both spatially and in terms of species composition.

The lowland region is dominated by the alien *Pelophylax* sp. and secondarily by *B. viridis* and *H. intermedia*, while the other species are entirely marginal. The Po Valley is strongly human-dominated and the species most sensitive to habitat alteration are rare and isolated, while the most adaptable ones can still be widespread (Ficetola & de Bernardi, 2004). In this study, this trend is confirmed, showing a strong homogenization of the amphibian community in the Po Valley. In the

transitional region, the most common species by far is still *Pelophylax* sp., but there is a turnover among the other common species (17%: *R. dalmatina*; 10%: *B. bufo* and *L. vulgaris*; 7%: *T. carnifex*). This assemblage includes widespread species with great distribution range both at the Italian level and at the European level (considering the *Triturus cristatus* superspecies for *T. carnifex*). These species are theoretically quite tolerant and adapted also to lowland environments, but the intensive agriculture and the subsequent loss of habitat and isolation can strongly threaten them and lead to local extinction (Ficetola & de Bernardi, 2004). These phenomena are exacerbated by the presence of alien species and fishes in general, which are a

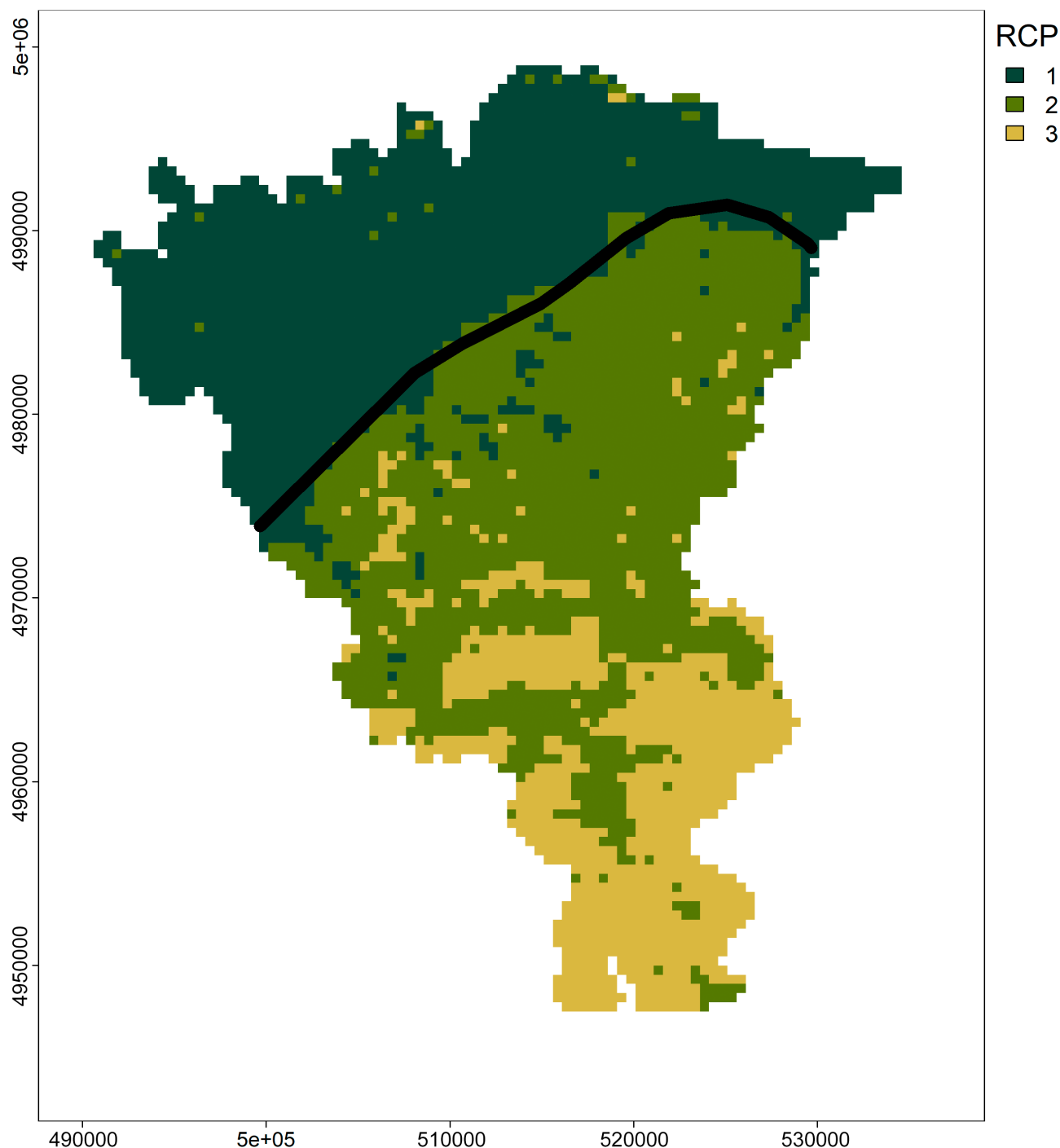


FIGURE 5 Map of the three regions of common profile (RCPs) in which the study area is divided. The thick black line represents the boundary between the Po Plain Province and the Apennine Province. The color palette was obtained with the R package *scico* (Pedersen & Crameri, 2018).

major driver of population dynamics of newts in the Po Plain (Falaschi et al., 2022). Finally, *I. alpestris* is the most common species in the Apennine region, followed by two amphibians inhabiting the Apennine streams: *S. salamandra* and *R. italica*. Besides these species, *B. bufo* and *R. dalmatina* also occur with a fair probability. In conclusion, the RCP approach clearly defined three regions: the lowland region, which harbors amphibian species

adapted to agricultural areas; the transitional region, which hosts species not tied to a specific altitude or predominantly to the lowlands and once widespread also in the Po Valley; and the purely Apennine region, inhabited by mountainous and forest taxa.

According to the ecoregions from Blasi et al. (2018), the lowland region is included in the Po Plain Province while the transitional and Apennine regions lie in the

Apennine Province. This is consistent geographically but allows us to highlight an interesting phenomenon at the level of community composition. While the plain region is homogenized and even quite tolerant and lowland adapted species such as *B. bufo*, *R. dalmatina*, and *L. vulgaris* are very rare there, such species are hosted in the Apennine, becoming the most common ones in its lower part, where the most typical and upland species still fail to prevail. Decline and vanishing of amphibians, including widespread ones, is a recurring pattern in intensively cultivated lowlands in Europe (Arntzen et al., 2017; Renoirt et al., 2024). The Po Plain is one of the most urbanized and cultivated areas in Europe (Romano & Zullo, 2016), and some of its most iconic amphibian taxa are declining and threatened with extinction (Andreone et al., 2004; Falaschi et al., 2022; Ficetola et al., 2023; Rondinini et al., 2022). In the case of this study, the contiguity of the plain with the Apennine, affected by different trends (Falcucci et al., 2007), makes it possible to maintain a region where species are still quite common in the study area.

A point of attention must be paid to the spread of the marsh frog (*P. ridibundus*). Until 2005, this invasive species was absent (Razzetti et al., 2010), and till 2016, it was restricted to the western part of the study area (Falaschi et al., 2018), while it is now dominant everywhere but the highest peaks. This spread poses a threat to native amphibians because the marsh frog's broad environmental niche overlaps with theirs (Pille et al., 2024). This species is able to colonize even the Apennine streams and the ongoing global warming could foster its propagation in areas where it is currently absent (Falaschi et al., 2018; Padilla et al., 2023). The true impact on the native amphibian species in the study area would warrant a more detailed analysis, including population-level studies.

In conclusion, we showed the potential of combining multispecies distribution models and bioregionalization at the local scale. HMSC can account for factors not explicitly integrated into the model and provide the basis for RCP identification, even at the local scale. A weak point of the HMSC framework is not directly accounting for imperfect detection, an important issue in ecological modeling, integrated even in some multispecies approaches (Doser et al., 2023; Rota et al., 2016). However, the framework's robustness has been recently tested, showing that 25% of missing data is fully tolerated, while just for estimating species niches and mapping distribution even 50% of data completion provides valid results (Romera-Romera & Nieto-Lugilde, 2025). Here, we targeted the surveys in order to maximize detection probability when possible and, although we cannot exclude bias, deriving also from species-specific detectability (Costa et al., 2025; Moor et al., 2024), we obtained ecologically

consistent results. Specifically, the most crucial climatic and land-use factors for amphibian species in an understudied but interesting region were identified. Understanding the drivers of species distribution and basically their habitat preferences can also be the basis for conservation and management actions (Cañadas et al., 2005; Gray et al., 2007; Sanderson et al., 2002). The subdivision of an area based on species' probability of presence can be important information for conservation planning too, as it allows reasoning in terms of species assemblages rather than individual species, without using a single "umbrella" species to represent all of them, at the risk of losing crucial information (Hill et al., 2017; Wang et al., 2021). Finally, having defined the distribution and composition of species assemblages in a fast-changing world can be an initial step in studying their shifts, both with a modeling and long-term study approach (Franklin et al., 2016; Miller et al., 2018).

AUTHOR CONTRIBUTIONS

Martino Flego: Conceptualization (lead); data curation (lead); formal analysis (lead), investigation (lead); methodology (lead); visualization (lead); writing—original draft (lead). **Alice Funk:** Data curation (equal); formal analysis (equal); investigation (lead); writing—review and editing (equal). **Thomas Dadda:** Investigation (equal); writing—review and editing (equal). **Valentina Rumo:** Data curation (equal); investigation (equal); writing—review and editing (equal). **Roberto Sacchi:** Funding acquisition (equal); supervision (equal); writing—review and editing (equal). **Marco Mangiacotti:** Conceptualization (equal); funding acquisition (equal); supervision (lead); writing—review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Flego, 2026) are available from Zenodo: <https://doi.org/10.5281/zenodo.20734800>.

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SUPPORTING INFORMATION

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

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