

RESEARCH ARTICLE

Acoustic species distribution models (aSDMs): A framework to forecast shifts in calling behaviour under climate change

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Abstract

1. Species distribution models (SDMs) are a key tool for biogeography and climate change research, although current approaches have some significant drawbacks. The use of species occurrence constrains predictions of correlative models, while there is a general lack of eco-physiological data to develop mechanistic models. Passive acoustic monitoring is an emerging technique in ecology that may help to overcome these limitations. By remotely tracking animal behaviour across species geographical ranges, researchers can estimate the climatic breadth of species activity and provide a baseline for refined predictive models. However, such integrative approach still remains to be developed.
2. Here, we propose the following: (a) a general and transferable method to build acoustic SDMs, a novel tool combining acoustic and biogeographical information, (b) a detailed comparison with standard correlative and mechanistic models, (c) a step-by-step guide to develop aSDMs and (d) a study case to assess their effectiveness and illustrate model outputs, using a year-round monitoring of calling behaviour of the Iberian tree frog at the thermal extremes of its distribution range. This method aims at forecasting changes in environmental suitability for acoustic communication, a key and climate-dependent behaviour for a wide variety of animal taxa.
3. aSDMs identified strong associations between calling behaviour and local environmental conditions and showed robust and consistent predictive performance using two alternative models (regression and boundary). Furthermore, these models better captured climatic variation than correlative models as they use observations at higher temporal resolution. These results support aSDMs as efficient tools to model calling behaviour under future climate scenarios.

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4. The proposed approach offers a promising basis to explore the capacity of vocal species to deal with climate change, supported by an innovative integration of two disciplines: bioacoustics and biogeography. aSDMs are grounded on ecologically realistic conditions and provide spatially and temporally explicit predictions on calling behaviour, with direct implications in reproduction and survival. This enables to precisely forecast shifts in breeding phenology, geographic distribution or species persistence. Our study demonstrates how acoustic monitoring may represent an increasingly valuable tool for climate change research.

KEYWORDS

animal behaviour, bioacoustics, biogeography, climate change, ecoacoustics, ecological niche, environmental suitability, passive acoustic monitoring

1 | INTRODUCTION

Climate change is a critical challenge for biodiversity, as it imposes shifts in geographical ranges, phenological patterns, species interactions and might eventually result in species extinction (Dawson et al., 2011; Pecl et al., 2017). To identify proper conservation actions, it is paramount to assess climate change impacts on biodiversity, and the use of monitoring and predictive techniques plays a major role in this urgent task. Species distribution models (SDMs) are widely applied to forecast climate change-driven shifts in species range, by following two alternative strategies: correlative and mechanistic approaches (Kearney et al., 2010). Here we propose a new development based on the integration of bioacoustics and biogeography that provides a robust and cost-effective tool to expand SDMs, leveraging the advances in passive acoustic monitoring (PAM), while addressing some of the drawbacks of these modelling methods.

Whereas the correlative approach combines readily available biogeographical and environmental data to model species distributions (Rodríguez-Rodríguez et al., 2020), the mechanistic one offers a process-based approach to better examine the potential response of species to changing environments (Peterson, 2011). Biogeographical data are a key, but incomplete proxy for environmental suitability and species persistence, especially when considering presence-only data (Villén-Pérez & Carrascal, 2015). For instance, source-sink dynamics may yield presence records in unsuitable habitats (sinks), supported by individual dispersal from high quality habitats (sources), which reveals the limitation of presence records to predict habitat suitability (Schurr et al., 2012). The mechanistic approach has been proposed to overcome some of these shortcomings, allowing to forecast species response to current and novel environmental conditions. However, this requires species-specific physiological data and complex biophysical models (i.e. based on individual-level flows of mass and energy; Kearney et al., 2010) that are only available for a limited subset of species, a shortage of eco-physiological information constraining the broad application of these mechanistic models (Bovo et al., 2018).

Passive acoustic monitoring is an emerging technique to remotely track animal communities and ecosystems (Gibb et al., 2019; Sethi et al., 2018; Sugai et al., 2019) that increases our capacity to assess

biodiversity in time and space. Using acoustic sensors, PAM captures environmental sounds to characterize multiple aspects of communities and species (Gibb et al., 2019; Sueur & Farina, 2015). Animal sounds are species-specific and mediate vital behaviours, such as courtship, feeding or territory display (Bradbury & Vehrencamp, 1998; Fletcher, 2007; Gerhardt & Huber, 2002), hence they not only inform us about species presence or abundance but also about their behavioural and physiological status (Gibb et al., 2019). As sound production is highly dependent on environmental conditions (Krause & Farina, 2016; Llusia, Márquez, Beltrán, Moreira, et al., 2013), besides it can be used as an indicator of species persistence under climate change.

In combination with niche modelling, these novel techniques may assist researchers in providing a basis for the development of new species distribution models: aSDMs. Recent studies have shown how acoustic monitoring can be used to estimate climatic breadth and environmental suitability for calling behaviour (Bonnefond et al., 2020; Llusia, Márquez, Beltrán, Benítez, et al., 2013), laying the foundations for aSDMs. These estimates constitute a novel source, not only of eco-physiological information to model species distribution, but also behavioural and phenological information, improving our tools to predict past, present and future environmental suitability for vocal animals. aSDMs are suited for a wide range of taxa that rely on sounds for communication and orientation such as anuran amphibians, birds, mammals or some invertebrates (Gibb et al., 2019). Therefore, niche modelling based on acoustic monitoring may help to overcome some of the current shortfalls of the correlative and mechanistic approaches (e.g. limitations of presence-only data, shortage of eco-physiological information), while providing accurate and meaningful predictions under global change scenarios.

Although the potential contribution of PAM in biogeography and climate change research have recently been advocated (e.g. Krause & Farina, 2016; Lomolino et al., 2015; Sueur et al., 2019), its practical application still demands well-defined methodological frameworks and robust modelling tools. The development of aSDMs attempts to fill this gap and promote new research directions. Thus, some of the primary questions to resolve are as follows: (i) What are the data requirements for such an approach? (ii) How to select study species and monitoring sites? (iii) What types of analyses are needed to retrieve acoustic data?

(iv) How to link acoustic, environmental and biogeographical data to predict climate-driven shifts in species distribution and phenology?

In this paper, we address all these points and outline a general and transferable methodological framework to build novel SDMs based on the integration of bioacoustics and biogeography. We provide a detailed step-by-step description to build aSDMs, a study case to evaluate their effectiveness and illustrate model outputs, as well as datasets and R code to implement this new method. Finally, we compare the key features of aSDMs to correlative and mechanistic approaches, and discuss their benefits, limitations, and prospects.

2 | ACOUSTIC SPECIES DISTRIBUTION MODELS: METHODOLOGICAL FRAMEWORK

The acoustic SDM combines acoustic and biogeographic information aiming at assessing the environmental suitability for calling behaviour and forecasting both geographical and phenological shifts under climate change scenarios. Our framework relies on acoustic monitoring and local environmental variables to build models that estimate calling probability and provide spatially and temporally explicit predictions of behavioural responses to climate change, including climate-driven shifts in breeding phenology, geographic distribution and species persistence. This framework is composed of nine steps (Figure 1) and has been developed to be modular and customizable to specific requirements of species and questions of interest. In this section, we provide methodological details and recommendations for study designs.

2.1 | Step 1. Selection of the study species

These new SDMs are designed for species using acoustic communication, such as grasshoppers, crickets, katydids, cicadas, teleost fish, anuran amphibians, crocodiles, geckos, turtles, tortoise, terrestrial and marine mammals, passerines and other birds (Bradbury & Vehrencamp, 1998). Data collection, modelling and interpretation of predictions are based on animal sound production, and therefore two initial criteria should guide the selection of the study species: (i) species emitting acoustic signals related to vital functions such as breeding, feeding or navigation, so that signalling activity can be monitored and aSDMs forecast climate-driven changes in those behaviours and (ii) taxa using species-specific and described signals that can be recorded, detected and correctly identified. As this method benefits from prior information on the species distribution (e.g. to locate populations at climatic extremes), an additional criterion is to select (iii) taxa with well-established taxonomic status and well-documented geographic ranges.

2.2 | Step 2. Selection of the monitoring sites

aSDMs apply a cross-site comparison (Weltzin et al., 2003) to examine the species response to climate, by monitoring calling activity

along environmental gradients. The location of the study sites should be chosen to represent as many distinct climatic or environmental conditions as possible, while remaining feasible. Designing spatial coverage requires to address trade-offs between affordability and data comprehensiveness (Sugai et al., 2020). One way to achieve this is to target sites located at the extremes of an environmental gradient (e.g. cold vs. warm extremes; dry vs. wet extremes, or sites with distinct multi-dimensional parameters identified with a clustering approach), hence covering most of the range of climatic variation experienced by the study species to approach the environmental breadth of their calling behaviour. It has been demonstrated that examining the performance of the study species at contrasting climatic conditions can contribute substantially to assess the influence of climate on calling behaviour, even when monitoring only two populations (Bonnefond et al., 2020; Llusia, Márquez, Beltrán, Benítez, et al., 2013; Llusia, Márquez, Beltrán, Moreira, et al., 2013).

Overall, we recommend to follow five major criteria when selecting monitoring sites: (i) sites located at the climatic extremes of the species ranges, ideally within the 10% highest/lowest values (Llusia, Márquez, Beltrán, Benítez, et al., 2013); (ii) sites where the study species is common to ensure that enough signalling events are collected; (iii) sites with relatively low sound pressure levels from geophony (non-biological sounds from natural origins; for example, strong winds, or turbulent rivers) to facilitate signal detection and identification (Ulloa et al., 2021); (iv) sites with relatively low anthropogenic disturbances (including noise caused by humans such as road traffic noise) to prevent alterations of the species behaviour (Brumm, 2013), and (v) relatively accessible sites to facilitate setting up and maintenance of the equipment.

To meet these standards and properly select monitoring sites for aSDMs, we suggest a detailed preliminary analysis. First, a list of candidate sites should be selected based on species distribution and climate information. We propose a simple procedure implemented in R to identify sites at climatic extremes (see `codeS1_finding-extremes.Rmd`; Desjonquères et al., 2022), using the Worldclim bioclimatic database (e.g. BIO1, BIO5, BIO12 and BIO16) and species geographical information (e.g. polygons) provided by the IUCN Red List. Finally, literature revision, expert panels and/or pilot fieldwork can be conducted to choose monitoring sites among the initial candidates according to the other criteria (i.e. species abundance, noise, disturbance and accessibility).

2.3 | Step 3. Collection of acoustic recordings

Passive acoustic monitoring is the most reliable and affordable means to collect long-term observational acoustic data (Andreassen et al., 2014; Buxton et al., 2016; Carriço et al., 2019; Melo et al., 2021). This non-invasive technique relies on installing autonomous recording units to sample all the sounds emanating from an environment (Aide et al., 2013; Desjonquères et al., 2020; Gibb et al., 2019; Obrist et al., 2010), including the calling activity of the focal species. We recommend to extend the monitoring program for long periods (e.g.

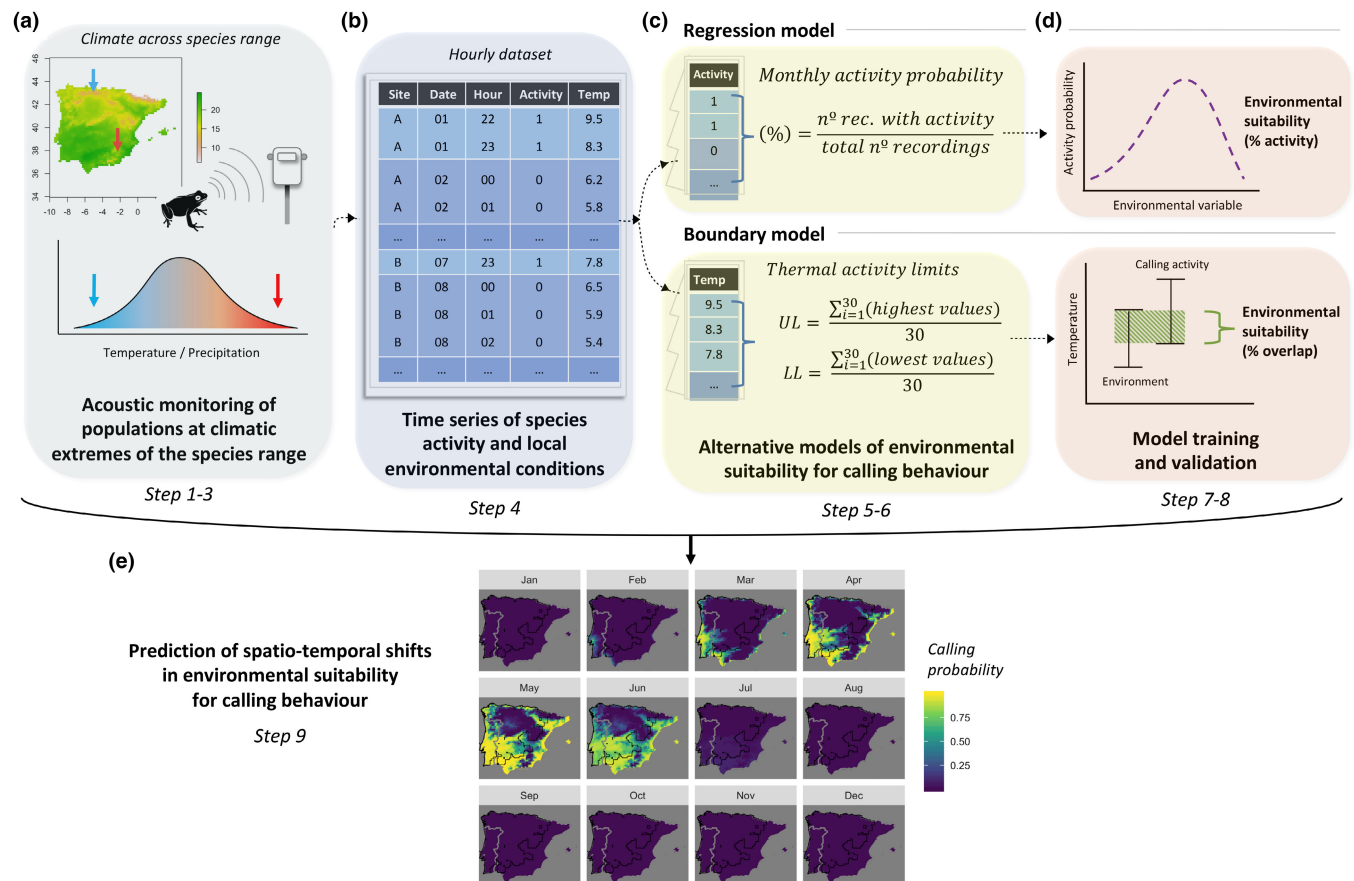


FIGURE 1 Schematic summary of the proposed framework to develop acoustic species distribution models (aSDMs) in nine steps: (a) passive acoustic monitoring (PAM) allows to track species activity along environmental gradients or at climatic extremes (steps 1–3); (b) acoustic analysis identifies species activity patterns over time (step 4); (c) the response and predictor variables are estimated by different approaches (steps 5–6), as calling probability over a given period (regression model) or as the upper and lower limits of environmental variables at which calling is observed (boundary model); (d) modelling fits the relationship between climate and behaviour and cross-validation assesses model predictive performance (steps 7–8); (e) models are applied to forecast spatio-temporal variation in environmental suitability for calling behaviour (step 9). The regression model relates calling probability and environmental variables with a generalized linear mixed models, while the boundary model estimates the percentage of overlap between the range of environmental conditions at a given period and the estimated species climatic breadth of calling behaviour.

at least a whole breeding season) to cover as much as possible the variability in species activity and weather conditions at the sites. To design the adequate sampling protocol, species calling behaviour, equipment autonomy and budget should be carefully considered, following available guidelines (e.g. Sugai et al., 2020).

2.4 | Step 4. Detection of acoustic activity

The extensive time-series of audio recordings obtained with PAM should be scrutinized to determine the species activity patterns. The presence-absence datasets are the easiest way to characterize calling activity and build aSDMs. Alternatively, the intensity of species activity can be determined with a relative abundance index such as the Vocal Activity Rate (Pérez-Granados et al., 2019) or the Amphibian Calling Index (Weir & Mossman, 2005), which quantify the level of acoustic activity (e.g. in the ACI, from 0 when no calls, up to 3 when full chorus). These datasets can be achieved by manual,

semi-automated or automated analysis, each approach having pros and cons. Manual identification usually shows higher accuracy but is highly labour intensive (Goyette et al., 2011), making this approach often unfeasible due to the enormous amount of data provided by long-term PAM. Semi-automated and automated signal recognition can be implemented using techniques such as machine learning (Ovaskainen et al., 2018; Pérez-Granados et al., 2019; Stowell et al., 2019) or acoustic indices (Indraswari et al., 2020), although this requires annotated datasets and complex programming. With the increasing availability of labelled species-specific data in sound libraries, for instance the Macaulay library (<https://www.macaulaylibrary.org/>) or Xeno-canto (<https://xeno-canto.org/>), and the development of open-source software (Araya-Salas & Smith-Vidaurre, 2016; Ulloa et al., 2021), it is expected that the implementation of these models will become easier in coming years. In semi-automated recognition, the identified sequences are typically validated by experts to reduce false-positive rates and improve the accuracy of the detection. Regardless of the analytical approach, it is important to ensure the

highest possible performance in species detection to reduce model uncertainty as the resulting datasets will then provide the basis for fitting aSDM.

2.5 | Step 5. Compilation of environmental information

A variety of model predictors can be considered to investigate the relationship between calling behaviour and climate, and these should be carefully selected according to the particular animal taxa under study. Temperature and precipitation are well-known drivers of animal activity in multiple species (Abram et al., 2017; Llusia, Márquez, Beltrán, Moreira, et al., 2013; Wong & Candolin, 2015) and are obvious primary candidates for any aSDM. In cases where ecological information about the species of interest is lacking, a multivariate approach (e.g. Principal Component Analysis) can be used to identify environmental gradients and reduce the dimensionality of the dataset (Manly & Alberto, 2016). Many other environmental factors might be worth adding, such as cloud cover, wind speed, as well as a range of habitat features, if available. These variables can be monitored at the study sites using on-site equipment (e.g. sensors), retrieved from nearby weather stations, or interpolated from climate datasets, which can even be validated or readjusted using locally monitored weather conditions.

When aSDMs intend to forecast potential environment-driven changes on behaviour, they require information on future conditions for each variable included in the model, which might limit the nature of the selected variables. In that case, the use of interpolated layers of climate in all modelling phases (training, validation and prediction) is generally advised (Hijmans et al., 2005). This allows to keep data standardized and at the right scale, and avoids mixing sources of information (e.g. on-site sensors and interpolated layers). However, to couple environmental and acoustic data for aSDMs, high temporal resolution data provided by weather station and on-site sensors will often be necessary. In that case, it is possible to combine environmental and acoustic data, as long as they are at comparable scales. Global climate and weather data are available at various spatial and temporal resolutions (from annual to daily), with predictions on future climate according to multiple global climate models and shared socioeconomic pathways (e.g. <https://worldclim.org>). These environmental variables can be rescaled to fit the temporal resolution of audio recordings or the desired resolution of analysis. Moreover, new variables can be computed considering time lags between weather conditions and species response.

In addition to climate data, the performance of aSDMs is presumably improved when including photoperiod as a model predictor because it strongly affects the onset and timing of multiple animal behaviours, especially in temperate and arctic species (Tsai et al., 2020). There are two independent aspects of photoperiod that may affect animal behaviour: day length and changes in day length (Figure S1). In many temperate regions, while day length and climate in spring may resemble those in autumn, the change in day length

progresses in the opposite direction, representing potential environmental cues to identify these seasons and to act as important landmarks for seasonal rhythms in many species (Tsai et al., 2020). When calling behaviour typically occurs in spring or autumn, we thus recommend using changes in day length and/or changes in temperature as model predictors, while in summer or winter calling activity will be best predicted using day length and/or temperature. These variables can be obtained from a variety of sources, including the R package *GEOSPHERE* that computes day length in function of latitude (Hijmans, 2019).

2.6 | Step 6. Combining acoustic and environmental datasets

Modelling requires the estimation of a response variable that fits with the scale of the predictors. PAM provides high temporal resolution data (e.g. hourly) that often mismatches coarser information on future climate (e.g. monthly). When combining acoustic and climate datasets, it is thus necessary to summarize data at the highest resolution to match data at the coarsest scale. Although it represents a loss of data resolution, we suggest rescaling information on animal activity patterns when calculating the response variable; for instance, by computing the number of recordings with calling activity over a given period (e.g. a month; see *Study case*), which can be seen as the probability of calling behaviour (or calling probability) over that period.

2.7 | Step 7. Modelling environmental suitability for calling behaviour

We propose two alternative approaches to estimate environmental suitability for calling behaviour of the study species and forecast climate-driven changes in animal acoustic activity: regression models and boundary models (Figure 1). The first approach is based on statistical regression analyses (e.g. generalized linear mixed models) that fits the relationship between calling behaviour (response variable) and environmental factors (predictors) at the specified temporal resolution. For this type of aSDM, the response might be calculated as calling probability (see previous step). The second approach aims at determining the environmental breadth of calling behaviour, based on the information collected across the species distribution (e.g. gradients, extremes, etc.), which is described as the range of environmental conditions (i.e. boundaries) in which acoustic activity is performed. The boundary approach estimates environmental suitability as the proportion of time (e.g. hours or days) with favourable conditions for calling (i.e. those within the environmental breadth of calling behaviour). This can also be calculated as the overlap between those ranges in a given period (see Figure 1). Although there must be other convenient ways to build aSDMs, we propose these two approaches as starting points for the development of this methodological framework (see *Study case* in Supporting Information for

full details). Potential avenues for improvement might include to model and account for biases on acoustic detection or other sources of model uncertainty.

2.8 | Step 8. Evaluation of model performance

Model validation is a crucial step to evaluate the reliability of the predictions. We recommend a repeated randomized cross-validation which allows to assess model predictions without requiring extra data or removing data for the validation set. This iterative resampling process randomly splits the original data into two samples (training and validation sets, e.g. 70% and 30% of days within each month respectively), subsequently used to fit the model (training) and to evaluate the model predictive performance for each estimate by comparing observed and predicted values for the new set (validation). This comparison can be conducted using correlation coefficients with continuous response variables (e.g. calling probability) or a confusion matrix and associated performance metrics in the case of categorical response variables (e.g. presence–absence of activity).

2.9 | Step 9. Prediction of behavioural estimates at spatio-temporal scales

Once models are fitted and their predictive capacity tested, we can apply them to project environmental suitability for calling behaviour at different spatial (i.e. geographical areas) and temporal scales (e.g. past, present and future scenarios). Spatial projections can be obtained using standard biogeographic tools in R such as the packages RASTER, MAPS, MAPTOOLS OR RGEOS (Bivand et al., 2019; Bivand & Rundel, 2017; Brownrigg, 2013; Hijmans, 2021), enabling spatial visualizations and generation of new datasets for further statistical analysis. As aSDMs are trained with a large environmental variation observed over time, they can likely be used to predict across environmental gradients found at large geographical regions without the need of extrapolation (see Section 4). Thus, aSDMs allow to compare current and future conditions for calling behaviour and to forecast potential climate-driven shifts in distribution and phenology, contributing to evaluate climate change impacts on biodiversity and address questions such as: are environmental conditions for calling behaviour expected to decline or improve? Is the breeding season or species range predicted to be shifted, reduced or expanded?

3 | STUDY CASE: THE IBERIAN TREE FROG

3.1 | Data collection

To illustrate how to build aSDMs, we used a dataset on calling behaviour of the Iberian tree frog (*Hyla molleri* Bedriaga, 1890). Based on a year-round acoustic monitoring of two populations located at

the thermal extremes of the species range, this dataset documents the temporal activity patterns (hourly presence–absence of calling activity) and local environmental conditions in 2007–2009 (Llusia, Márquez, Beltrán, Benítez, et al., 2013). We selected this model species for fitting, evaluating and projecting aSDMs by following all steps of the proposed framework (see previous section). Details and specifications of the methods can be found in Supporting Information.

3.2 | Model fitting

Calling activity of the Iberian tree frog was positively influenced by monthly temperature and photoperiod (Figure 2a–c). Increased environmental suitability for calling behaviour was observed with higher monthly minimum temperatures and larger amount of change in photoperiod, a consistent response found in both cold and hot populations (Table S1). The boundary model estimated the environmental breadth of calling behaviour of the study species, which ranged from 5.6 to 25.8°C of monthly minimum air temperature, from –14 to 156 s of monthly photoperiod change, and above a minimum precipitation of 29.5 mm (Figure 2d).

3.3 | Predictive performance

Overall, the two types of aSDMs (regression and boundary) performed well for predicting calling behaviour of the Iberian tree frog (Figure 3a). Observed and predicted calling probability were positively correlated in most iterations for both SDMs, though the regression model showed a higher predictive performance (mean correlation of 0.75 and significant positive correlations in 99.7% of the iterations) than the boundary model (0.50 and 85%; Figure 3a). The predictive performance of the regression model varied slightly over periods and populations. This model accurately estimated periods with no calling activity (August–December), yet its performance decreased during the breeding season (January–July). In general, calling probability was overestimated for the hot population, and slightly underestimated for the cold population (Figure 3b). Similar results were found when considering the observed calling probability as presence–absence data, with ROC AUC revealing an overall high performance, which was higher for the regression model (Figure 3c).

3.4 | Predicted shifts in environmental suitability for calling behaviour

The two aSDMs predicted fairly similar values of environmental suitability for calling behaviour across the species range and current and future climate scenarios. Under current conditions, calling probability was predicted to progressively increase from January to June and from southern to northern regions of the Iberian

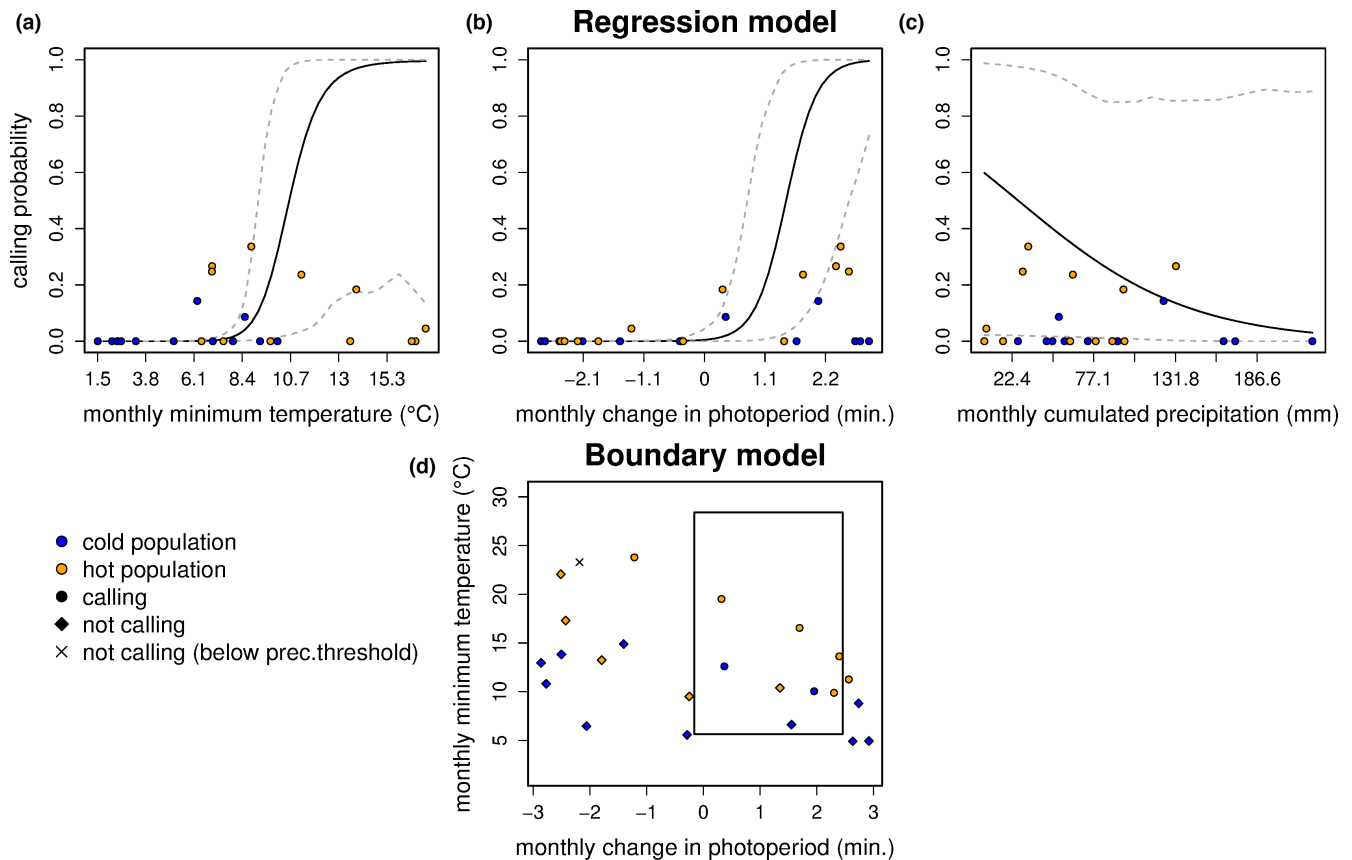


FIGURE 2 Effect of environmental factors on the monthly probability of calling activity of the Iberian tree frog (*Hyla molleri*), based on passive acoustic recordings in two populations located at the cold (blue) and hot (orange) extreme of the species distribution range, and estimated by the regression model (a–c; solid and dashed lines show the model prediction and 95% confidence intervals, respectively) and the boundary model (d; box shows the estimated species environmental breadth of calling behaviour).

Peninsula (Figures S2 and S3), in agreement with the breeding patterns of the Iberian tree frog (Llusia, Márquez, Beltrán, Benítez, et al., 2013). Under the RCP8.5 scenario, our aSDMs forecast improvements in the environmental conditions for calling activity over the entire year and across the species range for 2061–2080 (Figure 4 and Figure S4). Specifically, calling probability of the species is forecast to progressively increase in the future, from early winter (December–January) to early summer (June) following a southwest–northeast axis across the Iberian Peninsula (Figure 4 and Figure S4).

4 | DISCUSSION

We describe a novel framework to model species distribution and behaviour based on acoustic monitoring. This framework, termed aSDM, is the first practical proposal to break the ‘silence of biogeography’ (Lomolino et al., 2015). Our work provides a step-by-step guide for the application of aSDMs and demonstrates the efficiency of this tool to assess how climate change might drive spatial and temporal shifts in environmental suitability for sound production, a key adaptive behaviour for a variety of animals. Below we discuss the potential of aSDMs to overcome some drawbacks of the current

SDM approaches and outline challenges and directions for future research.

4.1 | Acoustic species distribution models in the context of biogeography

Forecasting species responses to climate change is a challenging task that has attracted considerable attention over the last decades (Pech et al., 2017). Biogeographical approaches accomplishing this goal have been classified either as correlative (when estimations are based on observational correlations) or mechanistic (when estimations are based on experimental data and explicit assumptions about underlying processes and mechanisms; Srivastava et al., 2019). Although correlative methods benefit from a wide availability of observational data and have been largely applied in biogeography, they are hardly ever generalizable to novel climates (Fernández & Hamilton, 2015; Townsend Peterson et al., 2007) and offer less understanding of the eco-physiological processes driving biogeographical shifts (Kearney & Porter, 2009). On the contrary, mechanistic models attempt to overcome such constraints by grounding their parameters on experimental data. Yet this approach also has limitations, as it provides less precision to predict ecological processes

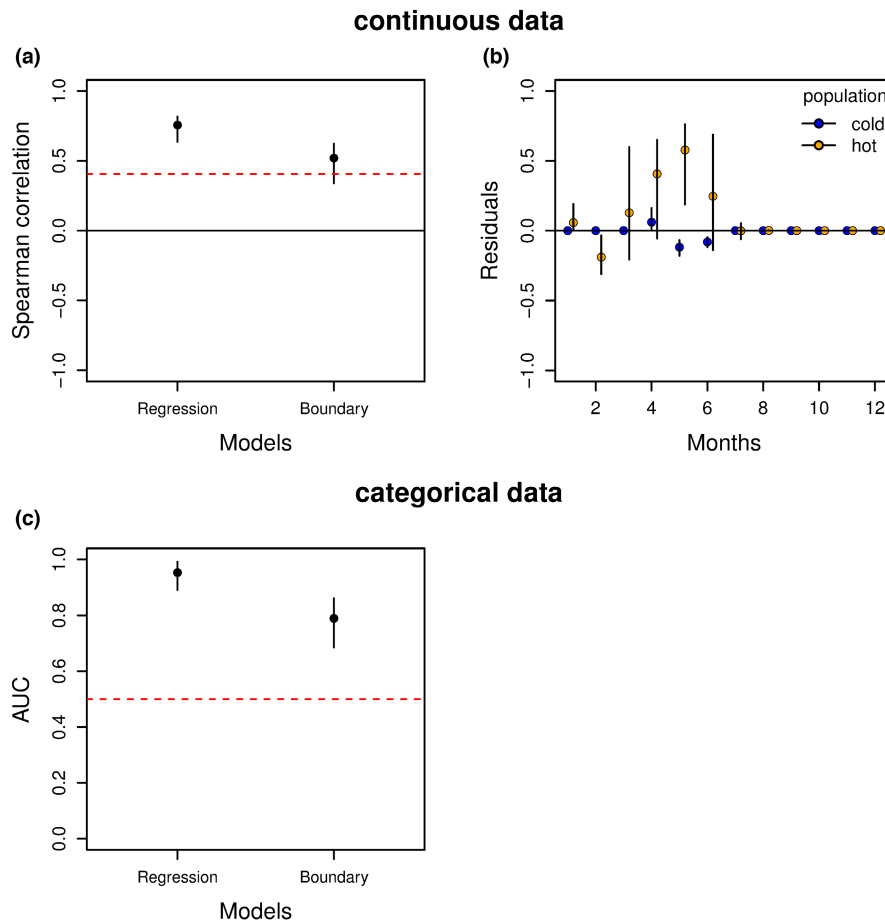


FIGURE 3 Predictive performance of the regression and boundary models based on continuous probability (a, b) and categorical presence–absence data (c). (a) Spearman correlation coefficients between observed and predicted calling probability per month (median and 95% confidence intervals), computed over 1000 iterations of random selection of training and validation sets (20–23 and 8 days per month, respectively; see Study case in Supporting Information). Red dashed line depicts significance threshold of the coefficients at the nominal level of 0.05. (b) Monthly residuals for the regression model. (c) Area under the curve (AUC) obtained from ROC curves based on the confusion matrices between observed and predicted calling probability per month (median and 95% confidence intervals), computed over 1000 iterations of random selection of training and validation sets (20–23 and 8 days per month, respectively; see Study case in Supporting Information). Red dashed line depicts an AUC of 0.5 indicating random predictions, while AUC close to 1 indicates highly accurate predictions.

under realistic conditions (Olsson & Jönsson, 2014), and its elevated costs prevent a wide application. Acoustic SDMs can be seen as an intermediate solution to deal with these drawbacks. In Table 1 and Table S2 we scrutinize similarities, differences and novelties of the aSDM approach in comparison with the long-established correlative and mechanistic approaches, following the detailed assessment provided by Kearney and Porter (2009) as a baseline.

As correlative approaches, aSDMs can be considered ecologically realistic because the observed response is limited by factors other than climate, such as biological interactions and other environmental determinants. Thus, in the context of the niche theory, aSDMs also estimate species realized niche (Pearson & Dawson, 2003; Table 1 and Table S2–(a,b,d,k)). Despite these similarities with correlative models, aSDMs strongly differ from them in their response variable. While correlative SDMs focus on species occurrence or abundance, aSDMs rely on the calling behaviour of the study species, which is monitored by automated acoustic sensors. Animal sounds are

frequently related to reproductive and social behaviour, as well as predator–prey interactions, playing a crucial role in fitness and survival (Fletcher, 2007). Thus, acoustic data have ecological and physiological implications (Sueur & Farina, 2015), comparable to that of mechanistic information (Table 1 and Table S2–(n)).

On the other hand, mechanistic SDMs are often based on thermal tolerance determined experimentally by sublethal endpoints and physiological critical thermal limits (i.e. CT_{max} and CT_{min}; Lutterschmidt & Hutchison, 1997); therefore, their predictions might be less conservative. Individuals performing highly energy-demanding behaviours (e.g. reproductive or calling activity) are likely constrained by narrower thermal bounds than those determined by sublethal endpoints. In this sense, aSDMs would lead to more realistic predictions for some species that rely on acoustic communication for mating, territory defence and other social and interspecific interactions. aSDMs can be applied to a variety of taxa, such as most mammals, birds, anurans and some insects. Besides, acoustic

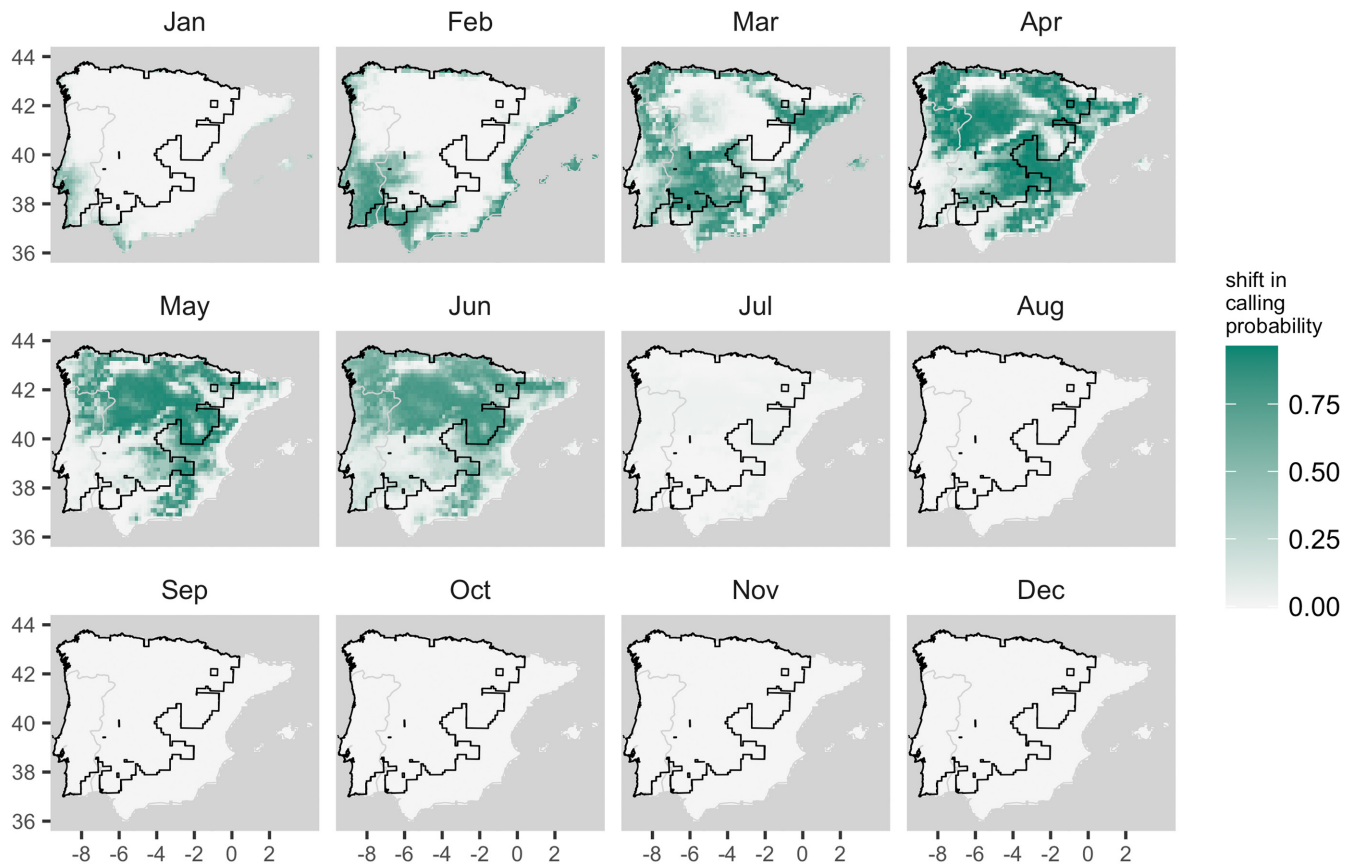


FIGURE 4 Spatio-temporal shifts in environmental suitability for calling behaviour of the Iberian tree frog forecast by the regression model under the RCP 8.5 climate change scenario (difference between current to 2061–2080 conditions). Predicted shifts can potentially vary from -1 to 1 , although the model only predicts positive values (depicted in dark green) in this case. Black polygons show the current distribution range of the study species in the Iberian Peninsula (Pleguezuelos et al., 2002).

sensors are cost-efficient tools that can provide information about whole acoustic communities, hence it likely reduces the effort and budget of gathering species-specific data in comparison with mechanistic approaches (Table 1 and Table S2—(f,g,n); Sugai et al., 2020). In summary, the acoustic approach can produce ecologically meaningful results with reasonable costs, increasing its applicability to a larger number of species and regions.

Another singularity of aSDMs is that they are built on samples collected at high temporal resolution. Passive acoustics enables to monitor animal activity over long periods (Andreassen et al., 2014; Buxton et al., 2016; Carriço et al., 2019; Sugai et al., 2020), capturing phenological dynamics and providing grounds for projecting phenological shifts across time and space (Sueur et al., 2019). This feature favours a higher resolution in the relationship between the climatic predictors and the response variable in comparison with correlative SDMs that often model species responses using a single observation per site and coarse resolution climate data. Moreover, this high temporal resolution enables aSDMs to assess the response of species across a wider range of climatic conditions than correlative SDMs. The variation in climatic conditions is better captured when monitoring sites located at the climatic extremes of the species range over long periods (e.g. a year, as in our study case) than when considering annual climatic averages across the species range (as in a typical

correlative model, Figure 5). Acoustic models are thus fitted with responses to a wider and higher-resolution range of environmental conditions than correlative models and, as a consequence, are likely better suited to forecast species distribution under novel conditions. The acoustic approach follows a time-for-space substitution logic rather than the space-for-time substitution strategy, characteristic of correlative models (Blois et al., 2013). By increasing the number of monitored sites, aSDMs may gain in spatial resolution (Table 1 and Table S2—(b,e,j,o)), a possibility that is becoming easier with ongoing technical advances in sound recording and automated analysis (see Section 4.3).

4.2 | Study case: Fitting a species distribution model

Based on a year-round PAM of two populations located at the thermal extremes of the geographic range of the Iberian tree frog, we demonstrate that the predictive performance of aSDMs is robust and consistent using two distinct approaches (regression and boundary models). The regression model fits a linear model to predict environmental suitability for calling activity, while the boundary model estimates an environmental breadth of this behaviour. The

TABLE 1 Features and advantages of the acoustic approach to develop species distribution models in comparison with correlative and mechanistic approaches, following the proposal by Kearney and Porter (2009). An extended version of this table is in Supporting Information (Table S2)

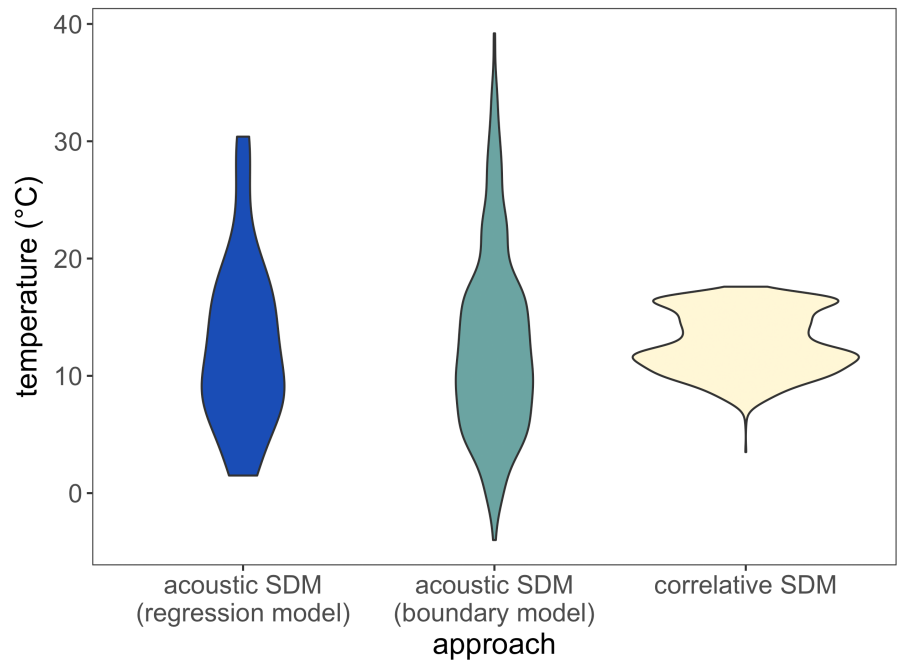
	Features	Advantages
(I) Conceptualization		
(a)	Theoretical basis	Same as correlative approaches
(b)	Approach and focus	Observational, acoustic activity
		Models based on realistic responses to environmental variation, specially not only across time but also across space
(c)	Model selection	Flexible
(d)	Generality (transferability) and precision (ecological realism)	Same as correlative approaches
		Same as correlative approaches
(e)	Scaling assumption	Time-for-space substitution: species temporal activity patterns determine spatio-temporal changes in their distribution
		Higher precision of phenological estimates
(II) Data requirements		
(f)	Focal species	Taxa producing airborne, substrate-borne or waterborne sounds
		Applicable to all species producing sounds
(g)	Species data	Acoustic data (sound presence, presence/absence or abundance)
		Data collection using non-invasive and cost-efficient methods (affordable for a large number of species)
(h)	Spatial data	Flexible
		Same as correlative approaches
(i)	Scale	Flexible
		Same as correlative approaches
(j)	Scale with highest resolution	Temporal scale
		Can capture phenological variation across space. Better capacity to afford predictions in novel climates than correlative approaches
(III) Model fitting		
(k)	Parameters	Dimensionless coefficients
		Robust because parameters are estimated from several acoustic datasets within several analytical frameworks. Realistic because they are estimated in natural conditions
(l)	Geographical variation (plastic and genetic)	Explicit (Acoustic monitoring of populations at distribution edges or across environmental gradients)
		Estimates behavioural responses in singular populations, which allow to assess inter-population geographic variation
(m)	Evolutionary change	Explicit
		Same as mechanistic approaches
(IV) Inference		
(n)	Output	Estimates of probability of calling behaviour (linked to fitness-related behaviours)
		Ecologically and behaviourally interpretable
(o)	Projection capacity	Spatial and phenological shifts
		Precise estimations of spatial and phenological shifts
(p)	Validation and evaluation	Same as correlative approaches
		Same as correlative approaches

regression model appears to have a slightly higher accuracy, probably because the estimated range of suitable conditions in the boundary model rely on the identification of extreme values that can be missed during data collection or when randomly selecting the validation dataset. Yet both models provided fairly consistent predictions of improvements of environmental conditions for the species calling behaviour under the RCP8.5 scenario. We recommend to select the model that best suits to the research questions: an assessment of the limits of a species niche may benefit from the boundary model, while the estimation of the probability of calling behaviour along an environmental gradient may require the regression model.

4.3 | Future challenges

Despite their advantages, the application of aSDMs faces some challenges that may be addressed by carefully directing current and future research efforts. First, the large time-series of passive acoustic recordings often require sophisticated sound analyses to estimate species activity patterns used to fit the predictive models. Considering the amounts of raw acoustic data, automated or semi-automated signal recognition methods are needed to mitigate such a time-consuming task (Aide et al., 2013; Andreassen et al., 2014). Some software (e.g.

FIGURE 5 Thermal amplitude captured by correlative and acoustic approaches, shown as violin plots. Temperature for the regression and boundary aSDMs corresponds to the values used in our aSDMs (see Study case in Supporting Information): Monthly and daily (respectively) maximum and minimum temperature at the two monitored populations. Temperature for the correlative SDMs corresponds to the values typically used to build such a model for the study species: Annual average temperature (WorldClim BIO1 layer) over the whole species range (Pleguezuelos et al., 2002).



Araya-Salas & Smith-Vidaurre, 2016; Ovaskainen et al., 2018; Ulloa et al., 2021) and species-specific recognizers are already available to apply automated signal detection with suitable efficiency (e.g. Potamitis et al., 2014; Ulloa et al., 2016). However, multiple factors typically challenge species detection in PAM recordings (e.g. noise from abiotic, biotic and anthropogenic sources; Priyadarshani et al., 2018). aSDMs will be reliant on the development of efficient automated analyses that allow to determine calling activity patterns from the avalanche of collected recordings.

Second, aSDMs will also benefit from an increased number of monitored populations and sites, so that datasets can achieve a better balance between temporal and spatial resolution of sampling. Our study case was based on two monitored populations of the Iberian tree frog at the thermal extremes of the species range. By increasing the number of monitored sites, researchers might include populations at the extremes of each environmental gradient included in the model. Ideally, aSDMs might also add replicates of each extreme or target site. This goal is expected to become realistic in the near future considering the current development of novel inexpensive recording units (Hill et al., 2018; Sethi et al., 2018; Whytock & Christie, 2017), as well as refined analyses. The design of a representative spatio-temporal coverage of environmental variation by targeting environmental extremes or gradients will increase the predictive performance of the acoustic approaches.

Finally, collaborative research networks and open-access data could remarkably contribute to spread the application of aSDMs for ecological and conservation purposes. Several long-term open-access PAM programs with wide spatial coverage have recently been launched (Roe et al., 2021) and might lay the foundations for the broad application of aSDMs. Following these initiatives, the bio- and eco-acoustic community should also develop platforms for data-sharing, making long-term acoustic datasets available to the entire scientific community. This resource may take inspiration from programs such as the GBIF to contribute to biogeographical research (Campos-Cerqueira & Aide, 2016). For example, long-established initiatives (e.g. Xeno-canto) and novel tools (e.g. eBird) could allow to support spatially explicit acoustic datasets over long periods and across species ranges. aSDMs will be instrumental in leveraging the potential of these platforms. Future research thus needs to further exploit the possibilities opened by aSDMs to better understand species distribution, behaviour, and phenology and the capacity of populations to cope with changing environmental conditions.

AUTHORS' CONTRIBUTIONS

Tabular author contributions modified after the CRediT system (<https://credit.niso.org/>). All authors contributed critically to the drafts and gave final approval for publication.

Contribution	Camille Desjonquères	Sara Villén-Pérez	Paulo De Marco	Rafael Márquez	Juan F. Beltrán	Diego Llusia
Conceptualization						
Data curation						
Formal analysis						
Investigation						
Visualization						

Contribution	Camille Desjonquères	Sara Villén-Pérez	Paulo De Marco	Rafael Márquez	Juan F. Beltrán	Diego Llusia
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Writing—review and editing						

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code supporting the results are available at <https://github.com/Desjonqu/aSDMs> and on Zenodo (Desjonquères et al., 2022; DOI: <https://doi.org/10.5281/zenodo.6584673>).

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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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