

1 **Species distribution modeling: a statistical review with**
2 **focus in spatio-temporal issues**

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8 **Abstract** The use of complex statistical models has substantially increased
9 lately in the context of species distribution behavior. This complexity has made
10 the inferential and predictive processes challenging to perform. The Bayesian
11 approach has become a good option to deal with these models due to the ease
12 with which prior information can be incorporated along with the fact that
13 it provides a more realistic and accurate estimation of uncertainty. In this
14 work, we firstly review the sources of information and different approaches
15 (frequentist and Bayesian) to model the distribution of a species. We also
16 discuss the Integrated Nested Laplace approximation as a tool for obtaining
17 marginal posterior distributions of the parameters involved in these models.
18 We finally discuss some important statistical issues that arise when researchers
19 use species data: the presence of a temporal effect (presenting different spatial
20 and spatio-temporal structures), preferential sampling, spatial misalignment,
21 non-stationarity, imperfect detection, and the excess of zeros.

22 **Keywords** Geostatistics · Hierarchical Bayesian models · INLA · Point
23 processes · Preferential sampling · SPDE

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1 Introduction

Understanding [spatio-temporal dynamics of species or diseases](#) is a key issue in many research areas such as ecology or epidemiology. Indeed, the so-called Species Distribution Models (SDMs), that link information on the presence/absence or abundance of a species to environmental variables to predict where (and how much of) a species is likely to be present in unsampled locations or time periods, are an important tool in many applied fields.

In the particular case of ecology, SDMs have been implemented in different theoretical and practical cases, including the identification of critical habitats ([Zhang , 2007](#); [Zhang et al. , 2008](#); [Paradinas et al., 2015](#); [Rufener et al., 2017](#)), the study of the risk associated with invasive species ([Fitzpatrick et al., 2007](#); [Luo and Opaluch , 2011](#)), the potential effects of climate change ([Iverson et al., 2004](#); [Araújo et al., 2005](#); [Brown et al., 2016](#)), the design of protected areas, the protection of threatened species ([Parviainen et al., 2008](#); [Roos et al., 2015](#)), [the distribution of bioclimatic indices](#) ([Barber et al., 2017](#)), the reintroduction of vulnerable species ([Danks and Klein, 2002](#); [Martinez-Meyer et al., 2006](#); [Hendricks et al., 2016](#)), the delineation of hot spots of biodiversity and species richness ([Jiménez-Valverde and Lobo, 2007](#); [Gotelli et al., 2009](#); [Goetz et al., 2014](#)), the potential distribution of infectious diseases ([Peterson et al., 2002](#); [Fatima et al., 2016](#); [Juan et al., 2017](#); [Martinez-Bello et al., 2017](#); [Martinez-Minaya et al., 2018](#)), among many others.

SDMs have also been used in many other contexts such as evolutionary biology, where they have been applied to topics such as speciation or hybrid zones ([Kozak et al., 2008](#)); in humans epidemiology, to predict the spread of diseases in humans ([Gosoni et al., 2006](#)), in veterinary epidemiology ([González-Warleta et al., 2013](#); [Barber et al., 2016](#)), in plants epidemiology ([Meentemeyer et al., 2011](#); [Václavík and Meentemeyer, 2009](#); [Neri et al., 2014](#); [White et al., 2017](#)), etc.

Different review papers about SDMs already exist (see for example, [Guisan and Thuiller, 2005](#); [Elith and Leathwick, 2009](#)), but most of them [are focused on the modeling of species data, keeping](#) a more general overview of the statistical critical issues. [Our intention in this review is to describe with more detail some of the statistical issues that arise when dealing with SDMs.](#)

In addition, nowadays the quantity and the quality of available datasets has substantially increased with respect to the last ten years, resulting in a higher complexity of the statistical issues that have to be addressed when a SDM is performed. Moreover, a detailed spatial and temporal description of the modeled phenomenon is becoming mandatory in many research fields from national and international organisms. Consequently to this increasing complexity, the performance of the SDM inferential and predictive processes are becoming more challenging, forcing researchers to develop new sophisticated statistical techniques. In line with this, new modeling approaches continue to be developed because using only geographic information systems (GIS) tools is not totally satisfactory for the type of usually available spatial data. Indeed, model complexity has generally increased over time from the use of

simple environmental matching (two good examples are BIOCLIM, Busby, 1991, and DOMAIN, Carpenter et al., 1993) to the use of models incorporating more complex non-linear relationships between species presence and the environment, such as generalized additive models (Guisan et al., 2002), neural networks (Park et al., 2003), or multivariate adaptive regression splines (Leathwick et al., 2005).

But more importantly, although most of the methods described in previous reviews (see for example, Guisan and Thuiller, 2005; Elith and Leathwick, 2009) have increased in their complexity, they are based on the [assumption](#) that the observations are [conditionally-independent](#), while species distribution data often depict [residual spatial autocorrelation](#) (Kneib et al., 2008; Beale et al., 2010). [In this review, we will focus on the fact that the spatial](#) autocorrelation should be taken into account in species distribution models, even if the data were collected in a standardized sampling, since the observations are often close and subject to similar environmental features (Muñoz et al., 2013). Other complications also arise in the modeling of the species due to imperfect survey data such as observer error, gaps in the sampling, missing data, the spatial mobility of the species (Latimer et al., 2006) and the fact that data have been collected through long periods of time. As a consequence, ignoring these issues in this type of analysis could lead to misleading results.

In line with this, the use of spatial and spatio-temporal models has grown enormously, allowing the incorporation of all these issues in the modeling process (Banerjee et al., 2014). Although there are other types of spatial data that could describe the behavior of a species (see for instance, Gelfand et al., 2010, for a detailed description of the three types of spatial data), [we will focus in this review](#) on geostatistical or point-referenced data, that come from those situations where the interest is to analyze spatially continuous phenomena. Bearing in mind that we would like to include the effect of possible covariates in the modeling or either to apply it to situations in which the stochastic variation in the data is known to be non-Gaussian, we will deal with the model-based geostatistics approach (Diggle and Ribeiro, 2007).

This combination of non-Gaussian data, a linear predictor and unobserved latent variables usually makes estimation and prediction computationally difficult. Bayesian inference turns out to be a good option to deal with spatial hierarchical models because it allows both the observed data and model parameters to be random variables (Banerjee et al., 2014), resulting in a more realistic and accurate estimation of uncertainty. Another advantage of the Bayesian approach is the ease with which prior information can be incorporated. Note that prior information can usually be very helpful in discriminating spatial autocorrelation effects from ordinary non-spatial linear effects (Gau-dard et al., 1999). But as usual in Bayesian complex models, inference needs numerical approaches. Among them, [in this review](#) we will emphasize [on](#) the use of the integrated nested Laplace approximation (INLA) methodology (Rue et al., 2009) and software (<http://www.r-inla.org>) as an alternative to Markov chain Monte Carlo (MCMC) methods, the main reason being the speed of calculation.

To summarize, our intention in this review is to describe with more detail the main statistical issues that arise when dealing with these models. In particular, in Section 2 we focus on the statistical aspects of the available data, while Section 3 discusses the basic structure of these models and how to perform inference. In particular, we provide a critical review of the Bayesian approach along with a detailed description of INLA. Our review also includes a discussion on some of the particularities appearing when dealing with them, including temporal correlation, preferential sampling, spatial misalignment, non-stationarity, imperfect detection and excess of zeros in Section 4. Finally Section 5 concludes. It is worth noting that we have tried to be simple in the notation to be readable by a large community of scientists.

2 Sources of information in SDMs

SDMs require basically two types of data input: data describing the observed species' distribution, and those data describing the landscape and the environmental characteristics in which the species can be found. In this Section we first present biological data, i.e. the observed species distribution, and in the second place the environmental data and the usual covariates that characterize the species distribution.

2.1 Biological data

The first type of data, which usually represent the response variable, can be either presence-only (i.e. records of localities where the species has been observed), presence/absence (i.e. records of presence and absence of the sampling localities), abundance data (i.e. the quantity of the species at the sampling locations), or proportional data (i.e. the proportion of the species at the sampling locations). Consequently, biological data can be measured at nominal (e.g. presence/absence type), ordinal (e.g. ranked abundance), ratio (e.g. frequency of detection) or continuous (e.g. abundance, richness) levels, which impacts the selection of the appropriate types of modeling algorithms to use, and subsequently the measurement level of this kind of models (e.g. probability or suitability of occurrence, type, expected mean).

Presence-only data lack of absence observations making this type of dataset unsuitable for many of the commonly used species distribution algorithms, unless *pseudo-absences* are assigned to unsampled portions of the study area. Inclusion of *pseudo-absences* records can seriously bias analyses. Indeed, methods used to generate pseudo-absences and their effects on model performance are an open research field in the species distribution context (Barbet-Massin et al., 2012; Iturbide et al., 2015).

With respect to the abundance, it could be expressed as a continuous variable (biomass of the species) or as count data (number of individuals). Abundance data reflect the quantitative spatial distribution of the species

within the area of interest, while presence/absence information can be used as a measure of the relative occurrence of species, thereby giving a different approximation. Despite abundance data provide greater information for conservation and management objectives, they are less common, as occurrence data are easier and less expensive to be collected. Indeed, abundance estimations are sensitive to detectability, and sampling methods seldom detect all individuals present in an area. Consequently, many researches rely on approximations of species abundance from species occurrence, although the ability to infer abundance from such information has been questioned, because detection is not perfect and occurrence probability may not be linearly related to density (Nielsen et al., 2005; Joseph et al., 2006).

Proportional data are also widely used in many ecological processes. The traditional approach in ecology is based on Gaussian linear models with previous transformation in the proportions. However, model parameters cannot be easily interpreted in terms of the original response and measures of proportions typically display asymmetry, and hence, inference based on the normality assumption can be misleading (Ferrari and Cribari-Neto, 2004). Beta regression has lately appeared as a good alternative to deal with this type of data allowing bounded estimates and intervals with model parameters that are directly interpretable in terms of the mean of the response (Paradinas et al., 2016, 2018).

It is also worth noting that different species do not behave independently among them. There are several species whose abundance (or presence) is constrained by competition: a large increase in one is unavoidably linked to declines of others. In these cases, the response variable should be considered using a joint distribution, and the models used for this type of data are known as joint species distribution models (Clark et al., 2014; Pollock et al., 2014; Hui, 2017; Taylor-Rodriguez et al., 2017).

All these types of biological data describing the [observed](#) species distribution can be obtained in a variety of ways such as museum collection, designed field surveys, from related activities (i.e. fisheries) or on-line resources.

2.2 [Environmental data](#)

With respect to the explanatory variables that could help to describe the species behavior, a wide range of environmental variables have been usually incorporated in SDMs. These variables are commonly related to climate (e.g. temperature, precipitation), topography (e.g., elevation, aspect, bathymetry, slope of the seabed), land cover type or seabed type in marine ecosystems. Variables tend to describe primarily the abiotic environment, although there is potential to include biotic interactions within the modeling.

This type of variables could be collected in situ, but usually they are derived from remoted sensing data. CRU (New et al., 2002), WorldClim (Hijmans et al., 2005), and MARSPEC (Sbrocco and Barber, 2013) are all examples of spatially explicit datasets of climatic remote sensing conditions. These datasets

encompass climatic information based on interpolations from global weather stations. However, interpolations are only as good as the underlying data, and uneven geographical coverage leads to high model uncertainty, especially in developing countries where few weather stations are in place (Daly, 2006; He et al., 2015). When uncertainty in spatial climate variables is not accounted for, coefficient estimates tend to be biased and this leads to poor performances of the SDMs, as shown recently with simulations by Stoklosa et al. (2015). This problem, also known as misalignment, is treated in this review in section 4.3.

3 Inference

In what follows, after presenting the traditional methods that have been used to perform inference in SDMs, we firstly discuss the hierarchical modeling as one of the most flexible and encompassing approaches to deal with them. The second subsection presents the Bayesian framework as a good option to deal with hierarchical models. The final subsection deals with the INLA approach for approximating the marginal posterior distributions of the parameters involved in the SDMs.

3.1 Gaussian Fields and Hierarchical modeling

A number of alternative modeling algorithms have been applied to classify species distribution as a function of a set of environmental variables. A first group of methods developed to deal with presence-only datasets includes maximum entropy algorithm, environmental distance, similarity, and envelope methods such as MAXENT (Phillips et al., 2006), Gower metric, Mahalanobis distance, and ecological niche factor analysis, all of which describe some measure of habitat suitability.

A second group involves machine-learning algorithms that are iterative in nature, such as artificial neural networks. These ensemble methods (e.g. Boosting Regression Trees, Classification Trees and Random Forests) generally involve developing multiple models on different subsets of the data, the results of which are averaged (Franklin, 2010).

A third group of methods is related to traditional regression and includes generalized linear models (GLM) and their non-parametric extension, generalized additive models (GAM), both of which can handle several measurement levels of the response variable by using a different link function (e.g. logistic for presence/absence or log for counts). GAM and a related method, multi-variate adaptive regression splines (MARS), are more flexible than GLM as they are fit using smoothing and piecewise linear splines, respectively, and are particularly useful for identifying the shape of species responses (Leathwick et al., 2005). MARS is computationally faster than GAM and the results are more easily converted to map predictions in a GIS; however, the currently used algorithms require normally distributed error terms. This makes MARS

unsuitable for use with presence/absence data unless the basis functions are extracted and used to parameterize a GLM (Leathwick et al., 2005). Rodríguez de Rivera and López-Quílez (2017) present a comparison of these three groups of methodologies stating that GAM models gave the best results.

However, most of the above mentioned methods are based on the assumption that the observations are conditionally-independent. But this is not always the case, as usually data of species distribution presents residual spatial autocorrelation (Kneib et al., 2008). GAMs and MARS can model spatial and temporal autocorrelation using smoothing splines. A very powerful and flexible alternative is to incorporate this spatial relationship by considering the species distribution data as point-referenced or geostatistical data. This type of data appears in those situations where the interest is to analyze spatially continuous phenomena. The most basic format for this kind of data is a pair composed by the spatial location coordinates defined throughout a continuous study region and the measurement value observed in the location. Geostatistical data require methods that allow to relate the species data with potential related covariates by quantifying the spatial dependence. However, one of the main interests in geostatistics relies on predicting the underlying process on those non observed locations (Cressie and Wikle, 2011; Banerjee et al., 2014).

Geostatistical or point-referenced data can be seen as realizations of a spatial process (random field) $\{y(\mathbf{s}), \mathbf{s} \in \mathcal{D}\}$ characterized by a spatial index \mathbf{s} which varies continuously in the fixed domain \mathcal{D} . This process is called a Gaussian field (GF) if for any $n \geq 1$ and for each set of locations $(\mathbf{s}_1, \dots, \mathbf{s}_n)$, the vector $(y(\mathbf{s}_1), \dots, y(\mathbf{s}_n))$ follows a multivariate Normal distribution with mean $\boldsymbol{\mu} = (\mu(\mathbf{s}_1), \dots, \mu(\mathbf{s}_n))$ and with covariance matrix $\boldsymbol{\Sigma}$ defined by a covariance function $\mathcal{C}(\cdot, \cdot)$, such that $\Sigma_{ij} = Cov(y(\mathbf{s}_i), y(\mathbf{s}_j)) = \mathcal{C}(y(\mathbf{s}_i), y(\mathbf{s}_j))$. If the mean is constant in space, i.e. $\mu(\mathbf{s}_i) = \mu$ for each i , and the generic spatial covariance matrix element depends only on the difference vector $(\mathbf{s}_i - \mathbf{s}_j) \in \mathbb{R}^2$, the spatial process is second-order stationary. In addition, if the covariance function only depends on the Euclidean distance $\|\mathbf{s}_i - \mathbf{s}_j\|$, the process is said to be isotropic.

In a hierarchical framework, the first step in defining a model for a random field is to identify a probability distribution for the observations available at n spatial locations and represented by the vector $\mathbf{y} = (y(\mathbf{s}_1), \dots, y(\mathbf{s}_n)) = (y_1, \dots, y_n)$ (the notation is simplified and the index i is used for denoting the generic spatial points \mathbf{s}_i). At the first level of the hierarchy, we usually select a distribution from the exponential family, characterized by a set of parameters. These parameters are linked with a linear predictor which also includes a latent GF denoted by $\xi(\mathbf{s})$ whose covariance function $\boldsymbol{\Sigma}$ depends on two parameters: σ^2 which represents the variance (partial sill in kriging terminology) and the range ϕ of the spatial effect.

Computational costs required to estimate these parameters are high when we deal with the spatial covariance function because the generated matrices are dense. This problem is known as “big n problem” (Banerjee et al., 2014; Jona Lasinio et al., 2012) and despite computational power today, it is still a computational bottleneck in many situations. A computationally effective

alternative is given by the stochastic partial differential equation (SPDE) approach proposed by Lindgren et al. (2011) (see Section 3.3).

In addition to the spatial pattern, the temporal variation could be equally important because the phenomenon can not only vary in space, but also in time (see Hefley and Hooten, 2016, for a comprehensive overview of modeling species distribution with a spatio-temporal perspective). Then, extending the spatial case to the spatio-temporal case including a time dimension, the process indexed by space and time can be defined as $\{y(\mathbf{s}, t), (\mathbf{s}, t) \in \mathcal{D} \subset \mathbb{R} \times \mathbb{R}\}$, and is observed at n spatial locations and at T time points.

The general structure for modeling the spatial distribution of species is given by the following formulation and notation. If $\mathbf{y} = (y_1, \dots, y_n)$ represents the observed values of the corresponding response variable Y with mean $\boldsymbol{\mu} = (\mu_1, \dots, \mu_n)$, each μ_i can be easily linked to a structured additive predictor η_i through a link function $g(\cdot)$, so that $g(\boldsymbol{\mu}) = \boldsymbol{\eta}$. The structured additive predictor $\boldsymbol{\eta}$ accounts for the effect of various covariates in an additive way:

$$\eta_i = \beta_0 + \sum_{m=1}^M \beta_m x_{mi} + \sum_{l=1}^L f_l(z_{li}), \quad (3.1)$$

where β_0 corresponds to the intercept; the coefficients $\boldsymbol{\beta} = \{\beta_1, \dots, \beta_M\}$ quantify the (linear) effect of some covariates $\mathbf{x} = (\mathbf{x}_1, \dots, \mathbf{x}_M)$ on the response; and $\mathbf{f} = \{f_1(\cdot), \dots, f_L(\cdot)\}$ are unknown functions of the covariates $\mathbf{z} = (\mathbf{z}_1, \dots, \mathbf{z}_L)$, and can assume different forms such as smooth nonlinear effects of covariates, time trends and seasonal effects, random intercept and slopes as well as temporal or spatial random effects. Note that this general structure can also be seen as a Generalized Additive Mixed Model (GAMM). It is also worth noting that here it is assumed that covariates are observed at the same locations of the response variable. The situation where covariates are observed in different locations than response variable (misalignment) will be discussed in Section 4.3.

In many statistical applications, in particular, in SDMs, the model involves multiple parameters that can be regarded as related or connected in some way by the structure of the problem, implying that a joint probability model for these parameters should reflect their dependence (Gelman et al., 2014). It is natural to model such a problem hierarchically, with observable outcomes modeled conditionally on certain parameters, which in turn are given a probabilistic specification in terms of further parameters, adding various levels of the modeling and thus defining a hierarchical model (HM). Note that Hierarchical models provide a generalization of all the models here presented, and moreover that they are capable to deal with all types of the data that we could find when dealing with SDMs. Table 3.1 describes all the models mentioned in this subsection along with a diagram emphasizing their nested nature.

Although other approaches can be used such as maximum likelihood (MLE; Le Cam, 1990), restricted maximum likelihood (RMLE; Bartlett, 1937), quasi-maximum likelihood (QMLE; Cox and Reid, 2004), the method of moments (Bowman and Shenton, 2006), the generalized method of moments (GMM;

Table 1 Matching of models presented and data types. LM: linear models. LMM: linear mixed models. GLM: Generalized linear models. GLMM: Generalized linear mixed models. AM: additive models. AMM: additive mixed models. GAM: Generalized additive models. GAMM: Generalized additive mixed models. HM: Hierarchical models. By construction, these models are nested: $LM < GLM < GAM < GAMM < HM$.

Explanatory Variable(s)	Response variable distribution	
	NORMAL	OTHER DIST. EXP. FAMILY
LP	LM	GLM
R. effects	LMM	GLMM
Non-Lin. effects	AM	GAM
R. effects + Non-Lin. effects	AMM	GAMM

Hansen, 1982), M-estimators (Shapiro, 2000), the maximum spacing estimation (MSE; Anatolyev and Kosenok, 2005), etc., in this work we will focus on the Bayesian approach to make inference for hierarchical models with a linear predictor of the form (3.1).

3.2 Bayesian approach

The use of the Bayesian framework as a way to make inference has increased in the last 50 years and it has been applied in different areas such as social sciences (Jackman, 2009), medicine and public health (Berry and Stangl, 1999), finance (Rachev et al., 2008), ecology (McCarthy, 2007), bioinformatics (Mallick et al., 2009), health economics (Baio, 2012), physical sciences (Andreon and Weaver, 2015) and econometrics (Gómez-Rubio et al., 2014). Bayesian reasoning is based on the [assumption](#) that parameters are treated as random variables, and prior knowledge has to be incorporated via the corresponding prior distributions of the said parameters. Bayes' theorem is the tool that combines prior information with the likelihood [yielding](#) the posterior distributions. It is worth noting that the Bayesian approach is perfectly suited for complex spatial models such as SDMs because it allows model parameters to be random variables, resulting in a more realistic and accurate estimation of uncertainty.

SDMs are a very good example of a hierarchical structure that can be expressed as a hierarchical Bayesian model (Wikle and Hooten, 2010; Hefley and Hooten, 2016). It can be structured in three levels: the first one refers to the data and is conditioned on the process and parameters in whatever aspects of the process are appropriate. The second level contains the latent components, which can be spatial and/or dynamic and the stochastic form can be univariate or multivariate. Finally, the third stage defines the priors for the parameters the latent processes depend on. The parameters in this level are also known as hyperparameters.

The most [commonly](#) approach used to perform Bayesian inference for spatial species distribution models are MCMC methods (Gelfand et al., 2006);

they are flexible computational tools which can be easily adapted to any kind of inferential problem. The most used software to implement MCMC algorithms are WinBUGS (Lunn et al., 2000; Brooks et al., 2011), OpenBUGS (Lunn et al., 2009) and JAGS (Plummer, 2016), which can also be run within other programs like R (through the R2OpenBUGS, R2WinBUGS, BRugs and rjags packages), Stata and SAS. Alternatively other R packages are BayesX (Brezger et al., 2003), CARBayes (Lee, 2013), stocc (for binary data only), spatcounts (for count data only), CARramps (for Gaussian data only), and spdep (for Gaussian data only). Several hierarchical processes including ecological processes (habitat suitability, spatial dependence and anthropogenic disturbance) and observation processes (species detectability) can also be performed using the hSDM package of R developed by Vieilledent et al. (2014). Functions in this R package use an adaptive Metropolis algorithm (Robert and Casella, 2011) in a Gibbs sampler (Gelfand and Smith, 1990) to obtain the posterior distribution of model parameters. The Gibbs sampler is written in C code and compiled to optimize computation efficiency. Thus, the hSDM package can be used for very large data-sets while reducing drastically the computation time. However, with hSDM it is not possible at the moment to model spatio-temporal or proportion response variables.

Despite of their generalized use, it is worth noting that MCMC methods still have many challenges to deal with (like the so-called “big n problem” mentioned above; see Banerjee et al. 2014; Jona Lasinio et al. 2012). Indeed, they can be extremely slow and even computationally unfeasible especially when the models are extremely complex (with many random effects or hierarchical levels) or when big datasets are considered in the space-time setting.

As a result, other options have appeared to make inference in SDMs. Taking advantage of the hierarchical structure of SDMs, Golding and Purse (2016) propose the use of an empirical Bayesian approach. In particular, they maximize the marginal posterior density of the model, which, in their words, enables the incorporation of prior knowledge over hyperparameters whilst being much less computationally intensive than fully Bayesian inference.

Here, we will focus on the integrated nested Laplace approximation (INLA) methodology (Rue et al., 2009), as a computational effective alternative to MCMC. Our choice is based on two facts: the speed of calculation and the ease with which model comparison can be performed.

3.3 INLA and SPDE framework

The INLA methodology is now a well established tool for Bayesian inference in several research fields, including ecology, epidemiology, econometrics and environmental science (Rue et al., 2017). It can be used through R with the R-INLA package. For more details about INLA for spatial and spatio-temporal models we refer the reader to Blangiardo et al. (2013) and Blangiardo and Cameletti (2015), where practical examples and code guidelines are also provided.

The reason underneath the possibility of using INLA is based on the fact that SDMs can be seen as latent Gaussian models (Rue and Held, 2005), the class of models INLA is designed for. After identifying the distribution for the observed data, we can link its corresponding mean to the linear predictor as in Eq.(3.1). If conditional independence is assumed, the distribution of the n observations is given by the likelihood

$$p(\mathbf{y} \mid \boldsymbol{\theta}, \boldsymbol{\psi}) = \prod_{i=1}^n p(y_i \mid \theta_i, \boldsymbol{\psi}) , \quad (3.2)$$

where $\boldsymbol{\theta}$ represents the set of latent (nonobservable) components of interest $\boldsymbol{\theta} = \{\beta_0, \boldsymbol{\beta}, \mathbf{f}\}$, also known as the latent field, and $\boldsymbol{\psi} = (\psi_1, \dots, \psi_K)$ denotes the vector of K hyperparameters. As we can observe in Eq. (3.2), each data point y_i is connected to one element θ_i in the latent field. This assumption can be relaxed and each observation may be connected with a linear combination of elements in $\boldsymbol{\theta}$ (Martins et al., 2013). In addition, the multiple likelihood case could also be taken into account.

In the context of latent Gaussian models, it is assumed a multivariate Normal prior distribution on $\boldsymbol{\theta}$ with mean $\mathbf{0}$ and precision matrix $\mathbf{Q}(\boldsymbol{\psi})$, i.e., $\boldsymbol{\theta} \sim \mathcal{N}(\mathbf{0}, \mathbf{Q}^{-1}(\boldsymbol{\psi}))$ with density function given by

$$p(\boldsymbol{\theta} \mid \boldsymbol{\psi}) = (2\pi)^{-n/2} |\mathbf{Q}(\boldsymbol{\psi})|^{1/2} \exp \left(-\frac{1}{2} \boldsymbol{\theta}' \mathbf{Q}(\boldsymbol{\psi}) \boldsymbol{\theta} \right) , \quad (3.3)$$

being $|\cdot|$ the matrix determinant and $'$ the transpose operation. When the precision matrix $\mathbf{Q}(\boldsymbol{\psi})$ is sparse a GF becomes a Gaussian Markov random field (GMRF, Rue and Held, 2005). Interestingly, when making inference with GMRFs, linear algebra operations are performed using numerical methods for sparse matrices and this gives rise to computational benefits.

In spite of the wide acceptance of INLA, its precision and its computational efficiency in many latent Gaussian models (see for instance, Martino et al., 2011; Schrödle et al., 2011; Ruiz-Cárdenas et al., 2012, for a description of how to use INLA in spatio-temporal disease mapping, in state-space models and in survival models, respectively), INLA cannot be directly applied when dealing with models that incorporate geostatistical data (that is, continuously indexed Gaussian Fields). The underlying reason is that a parametric covariance function needs to be specified and fitted based on the data, which determines the covariance matrix $\boldsymbol{\Sigma}$ and enables prediction in unsampled locations. But from the computational perspective, the cost of factorizing the dense covariance matrix $\boldsymbol{\Sigma}$ is cubic in its dimension. Despite computational power today, in many situations, it is still challenging to factorize it for computing the inverse and the determinant.

Lindgren et al. (2011) proposed an alternative approach by using an approximate stochastic weak solution to a Stochastic Partial Differential Equation (SPDE) as a GMRF approximation to a continuous Gaussian Field (GF) with Matérn covariance structure. Specifically, they used the fact that a Gaussian Field $\xi(\mathbf{s})$ with Matérn covariance is a solution to the linear fractional

SPDE

$$(\kappa^2 - \Delta)^{\alpha/2}(\tau\xi(\mathbf{s})) = \mathcal{W}(\mathbf{s}), \quad \mathbf{s} \in \mathbb{R}^d, \alpha = \nu + \delta/2, \kappa > 0, \nu > 0, \quad (3.4)$$

where Δ is the Laplacian, α controls the smoothness, κ is the scale parameter, τ controls the variance, and $\mathcal{W}(\mathbf{s})$ is a Gaussian spatial white noise process. The exact and stationary solution to this SPDE is the stationary GF $\xi(\mathbf{s})$ with Matérn covariance function given by:

$$\text{Cov}(\xi(\mathbf{s}_i), \xi(\mathbf{s}_j)) = \mathcal{C}(\xi_i, \xi_j) = \frac{\sigma^2}{2^{\nu-1}\Gamma(\nu)} (\kappa\|\mathbf{s}_i - \mathbf{s}_j\|)^{\nu} K_{\nu}(\kappa\|\mathbf{s}_i - \mathbf{s}_j\|), \quad (3.5)$$

being $\|\mathbf{s}_i - \mathbf{s}_j\|$ the Euclidean distance between two locations $\mathbf{s}_i, \mathbf{s}_j \in \mathbb{R}^d$, and σ^2 the marginal variance. Also, K_{ν} is the modified Bessel function of the second kind and order $\nu > 0$, which measures the degree of smoothness of the process. This parameter is usually kept fixed due to its poor identifiability. Conversely, $\kappa > 0$ is a scaling parameter related to the distance at which the spatial correlation becomes almost null, i.e., the range (for more information on the Matérn covariance model see Handcock and Stein, 1993; Stein, 1999). Typically, as it is pointed out in Lindgren et al. (2011), the empirically derived definition for the range is $r = \frac{\sqrt{8\nu}}{\kappa}$, with r corresponding to the distance at which the spatial correlation is close to 0.1, for each $\nu \geq \frac{1}{2}$.

The link between equations (3.4) and (3.5) is given by the expressions $\nu = \alpha - \frac{\delta}{2}$, and $\sigma^2 = \frac{\Gamma(\nu)}{\Gamma(\alpha)(4\pi)^{\delta/2}\kappa^{2\nu}\tau^2}$. In the particular case where the dimension is 2, i.e., $\delta = 2$, it follows that $\nu = \alpha - 1$ and $\sigma^2 = \frac{\Gamma(\nu)}{\Gamma(\alpha)(4\pi)\kappa^{2\nu}\tau^2}$.

Finally, in R-INLA, the Gaussian field $\xi(\mathbf{s})$ is found numerically as a weak solution to the SPDE in (3.4), and by default the smoothness parameter α is fixed to 2, corresponding with $\nu = 1$. With this assumption, the range is given by $\phi \approx r = \sqrt{8}/\kappa$, while the variance is given by $\sigma^2 = 1/(4\pi\kappa^2\tau^2)$.

Bayesian geostatistical analysis using R-INLA has been already applied in different contexts. Along with introducing the package `geostatsinla` for performing geostatistics with INLA in an easy way, Brown (2015) applies it in the context of mapping the *Loa loa* filiarasis disease (a dataset previously cited in Diggle and Ribeiro, 2007). Moreover, Karagiannis-Voules et al. (2013) have used Bayesian geostatistical negative binomial models to analyze reported incidence data of cutaneous and visceral leishmaniasis in Brazil covering a 10-year period, while González-Warleta et al. (2013) have used Bayesian geostatistical binomial models to predict the probability of infection of paramphistomosis in Galicia (NW Spain). In the context of fisheries, Bayesian geostatistical analysis using R-INLA has also been used to predict the presence/absence, the abundance, or the proportion of fish species (Muñoz et al., 2013; Pennino et al., 2013, 2014, 2016a,b; Paradinas et al., 2015, 2016; Cosandey-Godin et al., 2015; Quiroz et al., 2015; Roos et al., 2015; Rufener et al., 2017).

4 Extending statistical modeling of species distribution

There are a number of additional potential sources of bias and error that should be carefully considered when analyzing and modeling species distribution data. Errors may arise through the incorrect identification of species, or inaccurate spatial referencing of samples. Biases can also be introduced because collectors tend to sample in easily accessible locations. Here we discuss some of these issues.

4.1 Temporal autocorrelation

As above mentioned, in addition to the spatial pattern, the temporal variation could be equally important because the phenomenon can not only vary in space, but also in time. This happens in problems such as the evolution of epidemics (Stein et al., 1994; Hefley et al., 2017b), the spatio-temporal evolution of temperature (Hengl et al., 2012) or the understanding of the spatial dynamism of species over time (Wikle, 2003; Hooten et al., 2007; Hooten and Wikle, 2008; Paradinas et al., 2015, 2017; Williams et al., 2017).

As pointed out by Cressie and Wikle (2011), temporal correlation depends on the same principle as spatial correlation: temporally close observations tend to be more related than temporally distant observations. Consequently, model fitting and predictions improve when a temporal term is added. However, temporal and spatial scales are different and the spatio-temporal analysis is more complicated than the simple addition of an extra dimension to the continuous spatial domain.

In the context of species distribution modeling, most of the studies (surveys, plant coverage surveys, air pollution surveys, etc.) have been repeated periodically for long periods of time (Gitzen, 2012; Aizpurua et al., 2015). Although the main interest is the spatial evolution of the system under study, it must be taken into account that it varies not only in space, but also in time. Here we focus in this most common situation of discrete and regular time observations. For situations in which data are collected in irregular time-lags, that is, when the issue is handling continuous-time data, a good option is to consider 1D SPDE models with a second order B-Spline basis representation (Lindgren and Rue, 2008, 2015).

The spatio-temporal behavior of the data can vary depending on the nature of the process under study and the available sampling resolution. In particular, the basic model in (3.1) can be rewritten by splitting the f term into two terms, one indicating different possible spatio-temporal structures and another indicating any other latent model or non-linear effect. If y_{it} represents the response variable analyzed at location \mathbf{s}_i ($i = 1, \dots, n$) at time t ($t = 1, \dots, T$), then the mean of the response variable μ_{it} is linked to the linear predictor with

a link function $g(\cdot)$, as

$$\eta_{it} = g(\mu_{it}) = \beta_0 + \sum_{m=1}^M \beta_m x_{mit} + \sum_{k=1}^K f_k(z_{kit}) + u_{it} , \quad (4.6)$$

where β_0 corresponds to the intercept; the coefficients $\beta = \{\beta_1, \dots, \beta_M\}$ quantify the linear effect of some covariates on the response; u_{it} represents the spatio-temporal structure of the model; z_{kit} is the value of the k -th explanatory variable at a given location \mathbf{s}_i and time t ; and f represents any latent model applied to the covariates.

Among other structures, and following Paradinas et al. (2017), we just comment here four basic structures for u_{it} , each one allowing for different degrees of flexibility in the temporal domain of the spatio-temporal model. Paradinas et al. (2017) provide a figure that schematically illustrates all these structures:

- **Opportunistic spatial distribution:** this flexible structure consists in expressing u_{it} as different spatial realizations $\mathbf{w}_t = \{w_{1t}, \dots, w_{it}, \dots, w_{nt}\}$ of the same spatial field for each time unit t , while sharing a common covariance function (same κ and τ) to avoid overfitting:

$$\begin{aligned} u_{it} &= w_{it} , \\ \mathbf{w}_t &\sim \mathbf{N}(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) . \end{aligned} \quad (4.7)$$

This structure is a good approximation for processes where the spatial distribution varies considerably among different time units and unrelatedly among neighboring times. This structure has been used in Cosandey-Godin et al. (2015) and in Paradinas et al. (2015).

- **Persistent spatial distribution with random intensity changes over time:** when the pattern of spatial variation persists over time, but with possibly varying scales of intensity, a time structure is introduced in the model using a zero mean Gaussian random noise effect v_t . In this case, u_{it} is decomposed in a common spatial realization w_{it} along with an independent random noise effect v_t that absorbs the different mean intensities at each time t :

$$\begin{aligned} u_{it} &= w_{it} + v_t , \\ \mathbf{w}_t &\sim \mathbf{N}(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) , \\ v_t &\sim \mathbf{N}(0, \tau_v^{-1}) . \end{aligned} \quad (4.8)$$

For processes where the spatial component persists in time, this structure may be the most suitable. This structure has been used by Pennino et al. (2014) and in Paradinas et al. (2015).

- **Persistent spatial distribution with temporal intensity trend:** the process could show a temporal progression in its mean. To model that, a temporal trend effect $h(t)$ can be added to the linear predictor. In this case, u_{it} is decomposed in a common spatial realization w_i and an independent

temporal structured trend $h(t)$ to absorb the temporal progression of the process:

$$\begin{aligned} u_{it} &= w_i + h(t) , \\ \mathbf{w} &\sim \mathcal{N}(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) . \end{aligned} \quad (4.9)$$

This structure is highly recommended in situations where a temporal tendency is present. It was proposed by Paradinas et al. (2016) to identify intra-annual trends in fishery discards.

- **Progressive spatio-temporal distribution:** this structure incorporates both spatial and temporal correlation of the data to accommodate those cases where the spatial realizations change in a related manner over time. Here, u_{it} is decomposed in a common spatial realization w_{it} and an autoregressive temporal term r_{it} expressing the correlation among temporal neighbors of order K :

$$\begin{aligned} u_{it} &= w_{it} + r_{it} , \\ \mathbf{w}_t &\sim \mathcal{N}(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) , \\ r_{it} &\sim \mathcal{N} \left(\sum_{k=1}^K \rho_k r_{i(t-k)}, \tau_r^{-1} \right) . \end{aligned} \quad (4.10)$$

This structure is favored when the spatial realization varies between different times but not as much as in (4.8). Indeed, the structure has been used by Cameletti et al. (2011, 2013) and also by Cosandey-Godin et al. (2015).

Note that this list is just an overview of the different spatio-temporal structures which allow us to discern the nature of the general spatial behavior of the process over time. Unfortunately, the temporal resolution of spatio-temporal datasets is typically too low to fit most of the highly structured models.

4.2 Preferential sampling

In studies of species distributions, collecting data on the species of interest is not a trivial problem. With the exception of a few studies, species distribution models frequently rely on opportunistic data collection due to the high cost and time consuming nature of collecting data in the field, especially on a large spatial scale. As an example, studies on bird monitoring data are often collected by volunteers who concentrate the sampling process on areas where they expect to find species of interest. These types of opportunistically collected data tend to suffer from a specific complication: the sampling process that determines the data locations and the species observations are not independent (Diggle et al., 2010). Statistical models used for species distribution usually assume, if only implicitly, that sampling is non-preferential and that the selection of the sampling locations does not depend on the values of the spatial variable. However, opportunistic data are a clear example of preferential sampling, that occurs because sampling locations are deliberately chosen

in areas where the values of the species of interest are thought likely to be particularly high or low (Diggle et al., 2010).

Hence, applying standard geostatistical methods to preferentially sampled data potentially leads to biased results if the choice of monitoring locations is not accounted for in the modeling process. A possible approach to correct this issue is to interpret the data as a marked point pattern (Fortin and Dale, 2005; Diggle, 2013) where the sampling locations form a point pattern and the observations taken in those locations are the marks. By assuming that the intensity of the point process depends on the amount of species of interest, the marks and the pattern become not independent.

A preferential sampling model can be considered as a two part model that share information. Firstly, it is supposed that the observed locations $(\mathbf{s}_1, \dots, \mathbf{s}_n)$ come from a non-homogeneous Poisson process with intensity $\Lambda_i = \exp\{\alpha_1 + w_i\}$, i.e., a log-Gaussian Cox process (LGCP; Fortin and Dale, 2005; Diggle, 2013) is assumed, being α_1 the intercept of the LGCP and w_i the spatial effect of the model and $i = 1, \dots, n$ the index corresponding to the \mathbf{s}_i location. Secondly, the species characteristic (usually the abundance) y_i is assumed to follow an exponential family distribution (such as a Normal or a Gamma distribution when dealing with abundances, although clearly other options such as exponential, lognormal, etc., could be possible), whose mean is related with the spatial term using a link function $g(\cdot)$, $g(\mu_i) = \alpha_2 + \beta w_i$, being α_2 the intercept of the model and w_i the spatial term shared with the LGCP, but scaled by β to allow for the differences in scale between the abundances and the LGCP. More formally, the model can be expressed as follows:

$$\begin{aligned} y_i &\sim F(\mu_i, \gamma^2) \\ g(\mu_i) &= \alpha_2 + \beta w_i \\ \mathbf{w} &\sim N(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) \end{aligned} \tag{4.11}$$

where $\mathbf{w} = \{w_1, \dots, w_n\}$, the precision matrix $\mathbf{Q}(\kappa, \tau)$ is computed internally by the SPDE approach and represents the GMRF approximation to the continuous GF (see Illian et al., 2012; Krainski et al., 2017; Pennino et al., 2018, for details about how to implement these models within INLA), and $F(\mu, \gamma)$ represents a distribution coming from the Exponential family with mean μ and variance γ^2 .

4.3 Spatial misalignment

One of the crucial issues in studying the effect of environmental physical factors on species distribution concerns spatial misalignment (Clark and Gelfand, 2006; Gelfand et al., 2010) (Foster et al., 2012; Miller, 2012).

This occurs when the response biological variable (e.g. presence/absence of the species) is observed in locations which are different from the spatial points where covariate data are available. Additionally, it can happen that covariates have a different spatial scale if they are defined at the area or cell grid level (as in the case of remote sensing data).

The naïve solution to deal with spatial misalignment is represented by a two-stage approach: the first step consists in the prediction of the covariate in the spatial locations where the response variable is observed (through a geostatistical model by means of kriging or inverse-distance weighting) or in the downscaling of the gridded covariate to the point-level resolution (usually, it is considered the value of the cell where the spatial point is located). Then, at the second stage, these predicted values are plugged-in in the linear predictor (3.1) as known constants. The problem with this approach is that it doesn't take into account the uncertainty related to the covariate spatial estimation of the first stage, with the consequence of erroneous inference of the statistical model and a potential biased estimate of the environmental variable effect on the response variable (Foster et al., 2012).

A solution to incorporate the spatial prediction uncertainty in SDMs consists in implementing one of the so-called *errors-in-variables models* (Carroll et al., 2016) which can be estimated in a frequentist (by means of the EM-algorithm) or Bayesian framework (with MCMC or INLA). If we assume for example that the predicted covariate is a noisy version of the true one, a classical measurement error model can be adopted (Stoklosa et al., 2015). Otherwise, a Berkson-error model can be considered if the predicted covariate is a smoothed version (i.e. less variable) of the true variable (Foster et al., 2012). As reported in Stoklosa et al. (2015) “Which of these two types of error models to consider will depend on what the analyst believes to be the true underlying explanatory variable, and how the data were collected/measured. The analyst must take into account: how and whether the species responds to a particular climate observation (Berkson); or that it might respond to an average, such that relatively minor deviations from this are immaterial (classical)”.

Another alternative to the two-stage approach is the joint modeling strategy implemented in Barber et al. (2016) for evaluating the presence of the *Fasciola hepatica* in Galicia (Spain) using the annual mean temperature as covariate. In this case a spatial geostatistical model is specified for the covariate and is estimated jointly with the species distribution models in a Bayesian context. The joint model is specified as follows

$$\begin{aligned}
 y_i &\sim \text{Bernoulli}(\pi_i) \\
 \text{logit}(\pi_i) &= \beta_0 + \beta_1 \phi_i + w_i \\
 \mathbf{w} &\sim \text{N}(\mathbf{0}, \mathbf{Q}^{-1}(\kappa, \tau)) \\
 x_i &\overset{iid}{\sim} \text{N}(\phi_i, \sigma_x^2) \\
 \phi &\sim \text{N}(\mathbf{0}, \mathbf{Q}^{-1}(\gamma, \delta))
 \end{aligned} \tag{4.12}$$

where π_i is the probability of occurrence at site \mathbf{s}_i , x_i is the covariate of interest whose spatial distribution is specified through its mean (a realization of the Matérn Gaussian process ϕ depending on the parameters γ and δ), and through its variance σ_x^2 , which is introduced to express any possible measurement error. The model also includes another spatial process for the response represented by \mathbf{w} . This kind of model is part of the latent Gaussian model family and can be estimated using the SPDE-INLA approach (see Blangiardo and

Cameletti, 2015, Chap. 8 and Muff et al., 2015). The advantage is that this joint model [allows to properly propagate](#) all the uncertainty related to the covariate prediction; on the other side it can be extremely computationally expensive especially when there is more than one explanatory variable.

Finally, another alternative is the one proposed by Gómez-Rubio and Rue (2017) that, using a more general approach, deals with missing values in the covariates, based on fitting conditional latent Gaussian models where covariates are imputed using a Metropolis-Hastings algorithm.

4.4 Non-stationarity

The Matérn spatial covariance function $\mathcal{C}(\cdot, \cdot)$ specified by Eq. (3.5) enjoys the second-order stationarity [and isotropy](#) property, i.e. it depends only on the distance between the spatial locations and not on the direction or the coordinates. In some situations, this stationarity assumption, which is very convenient to simplify the inferential procedures, may not be suitable. For example, for some applications it is not realistic to assume that the spatial dependence structure is the same through the considered domain, especially when geographical elements or physical barriers (river, lakes, islands, etc.) exist. In such situations characterized by spatial heterogeneity and barriers, it may be more reasonable to adopt a non-stationary Gaussian field (see Gelfand et al. 2010, Chapter 9 and Risser 2016 for a review).

In ecological applications, heterogeneity in space (i.e. non-stationarity) occurs when a latent *global* process is also affected by some underlying local processes (Miller, 2012). A local modeling technique to include this heterogeneity in SDMs is given by the geographically weighted regression (GWR) characterized by covariate coefficients which vary spatially and are specific for each spatial location; a spatial kernel function is used to define spatial neighborhoods (see e.g. Brunsdon et al. 1998; Windle et al. 2010; Holloway and Miller 2015; Liu et al. 2017). Some authors do not completely agree with the use of these models due to the large degree of multicollinearity that their coefficients tend to exhibit, as well as strong positive spatial autocorrelation. As an alternative, spatial filtering provides a methodology for better dealing with multicollinearity, while accounting for spatial autocorrelation (see e.g. Griffith 2008). The Bayesian counterpart of GWR models, which are usually estimated by weighted least squares, is given by spatially-varying coefficients models (Gelfand et al., 2003; Finley, 2011).

In the SPDE framework non-stationarity is achieved by allowing the Matérn covariance function parameters to vary smoothly over space according to a log-linear function: thus, we will have $\sigma^2(\mathbf{s})$ for the marginal variance in (3.5) and $r(\mathbf{s})$ for the spatial range (Ingebrigtsen et al., 2014; Lindgren and Rue, 2015). Bakka et al. (2016) extend this approach to solve specifically the barrier problem for SDMs. In particular, they force the spatial correlation to go around the barrier (and not through them) by means of a partition of the considered spatial field- in a normal and in a barrier area - and in the specification of

two corresponding non-stationary processes with different range parameters (in particular for the barrier region the range parameter is almost zero). The application considered in Bakka et al. (2016) regards fish larvae data in the Finnish archipelago.

4.5 Imperfect detection

Detection in studies of species abundance and distribution is often imperfect due to observer error (Nichols et al., 2000), species rarity (Dettmers et al., 1999) or because detection varies with confounding variables such as environmental conditions (Gu and Swihart, 2004; Pennino et al., 2016b). When detection is imperfect, additional steps are usually needed to improve inference. Indeed, failure to do so could result in biased estimation and erroneous conclusions.

In the last years, new models called site-occupancy (Hoeting et al., 2000; MacKenzie et al., 2002) for presence-absence data and N-mixture models (Royle, 2004) for abundance data have been developed to solve this problem. These models combine two processes, an ecological process to describe habitat suitability and an observation process to take into account imperfect detection. To estimate detectability, these models use information from repeated observations at several sites. Detectability may vary with site characteristic such as habitat variables, or survey characteristics such as weather conditions, since suitability relates only to site characteristics. Different studies showing the advantages of site occupancy and N-mixture models over classical models that do not consider the problem of detectability can be found in the literature: Royle (2004); Dorazio et al. (2006) for birds, MacKenzie et al. (2002) for amphibians or Pennino et al. (2016b) for cetaceans. In addition to the detectability problem, a variety of methods have been developed to correct for the effects of spatial autocorrelation (Latimer et al., 2006; Johnson et al., 2013; Hefley et al., 2017a).

A Bayesian version for site-occupancy spatial models and N-mixture spatial models could also be implemented to take into account simultaneously both imperfect detection and spatial autocorrelation. To describe Bayesian site-occupancy spatial models, let z_i be a random variable describing habitat suitability at site s_i . It can take the value 1 or 0 depending on the habitat suitability, i.e. $z_i = 1$ or $z_i = 0$, thus a Bernoulli distribution is assumed with parameter π_i . Several visits at time $t = 1, \dots, T$ can happen at site i . Let y_{it} be a random variable representing the presence of the species at site i and time t . The species is observed at site i ($\sum_t y_{it} \geq 1$) only if the habitat is suitable ($z_i = 1$). The species is unobserved at site i ($\sum_t y_{it} = 0$) if the habitat is not suitable ($z_i = 0$), or if the habitat is suitable ($z_i = 1$) but the probability α_{it} of detecting the species at site s_i and time t is lower than 1. Then, y_{it} follows a Bernoulli distribution of parameter $z_i \alpha_{it}$, and the model is expressed as follows

Ecological process:

$$z_i \sim \text{Bernoulli}(\pi_i) , \quad (4.13)$$

$$\text{logit}(\pi_i) = \beta_0 + \sum_{m=1}^{M_1} \beta_m x_{mi}^{(1)} + w_i ,$$

Detection process:

$$y_{it} \sim \text{Bernoulli}(z_i \alpha_{it}) , \quad (4.14)$$

$$\text{logit}(\alpha_{it}) = \gamma_0 + \sum_{m=1}^{M_2} \gamma_m x_{mit}^{(2)} ,$$

where $\{\beta_0, \dots, \beta_{M_1}\}$ and $\{\gamma_0, \dots, \gamma_{M_2}\}$ are the parameters that quantify the linear effects of some covariates $(\mathbf{x}_1^{(1)}, \dots, \mathbf{x}_{M_1}^{(1)})$ and $(\mathbf{x}_1^{(2)}, \dots, \mathbf{x}_{M_2}^{(2)})$ in the ecological and observation process respectively. These covariates are usually variables referred to site characteristics such as habitat variables or survey characteristics such as weather conditions. $\mathbf{w} = (w_1, \dots, w_n)$ represents the spatial effect in the ecological process. Normally, this spatial effect is a Gaussian process that can be incorporated as geostatistical terms (in the way already introduced in Section 3), but other options are possible (such as CAR Normal distributions, as in Pennino et al. (2016b)). The R-package `hSDM`, which make inference using MCMC, can be used easily to fit some of these models. In addition, the `inlabru` package also handle the problem of detectability (Yuan et al., 2016).

With respect to N-mixture models, which are used for count data with imperfect detection, they implement a Poisson distribution for the ecological process, while using a Binomial distribution for the observability process (Royle and Nichols, 2003; Dodd Jr and Dorazio, 2004; Royle, 2004). The structure of the model is similar to site-occupancy model, in particular:

Ecological process:

$$N_i \sim \text{Poisson}(\lambda_i) , \quad (4.15)$$

$$\log(\lambda_i) = \beta_0 + \sum_{m=1}^{M_1} \beta_m x_{mi}^{(1)} + w_i ,$$

Detection process:

$$y_{it} \sim \text{Bernoulli}(N_i \alpha_{it}) , \quad (4.16)$$

$$\text{logit}(\alpha_{it}) = \gamma_0 + \sum_{m=1}^{M_2} \gamma_m x_{mit}^{(2)} .$$

The R-package `hSDM` allow us to fit some of these models. In addition, the INLA group is developing some methods to fit N-mixture models (Meehan et al., 2017).

4.6 Excess of zeros

The study of datasets with zero excess has a relevant role in the literature, particularly, in species distribution modeling (Agarwal et al., 2002; Ver Hoef and Jansen, 2007; Neelon et al., 2013), becoming highly relevant in last years indeed. Bayesian softwares like INLA already contain different functions to handle situations with zero excess. Generally, these situations are a source of overdispersion caused by a disagreement between the data and the distribution assumed: there are more zeros in the dataset than the proposed distribution could reasonably explain.

Zero-inflated models are a widely known tool for dealing with this problem. These models assume that the data follow a finite mixture of a degenerate distribution with all its mass at zero with a discrete distribution with support in $\mathbb{Z}^+ \cup \{0\}$ (Yau et al., 2003). If $1 - \pi_i$ represents the probability of species presence, π_i the probability of the species absence, i.e., $p(y_i|\pi_i) = \pi_i$ and $p(y_i > 0) = 1 - \pi_i$, and h a [probability mass function \(pmf\)](#) of some parametric discrete distribution with support on $\mathbb{Z}^+ \cup \{0\}$, the distribution of y_i has the following mixture density:

$$p(y_i|\pi_i, \mu_i, \boldsymbol{\psi}_1) = \pi_i \delta_0 + (1 - \pi_i) h(y_i|\mu_i, \boldsymbol{\psi}_1) , \quad (4.17)$$

being δ_0 the Dirac delta function, μ_i and $\boldsymbol{\psi}_1$ hyperparameters depending on h , and h is a [pmf](#) coming from a Poisson, binomial or negative-binomial ([note that this latter distribution is one of the usually considered to account for overdispersion](#)). The model is completed when linking π_i and μ_i with the linear predictors by means of:

$$\begin{aligned} \text{logit}(\pi_i) = \eta_i^{(1)} &= \alpha^{(1)} + \sum_{m=1}^{M^{(1)}} \beta_m^{(1)} x_{mi}^{(1)} + \sum_{l=1}^{L^{(1)}} f_l^{(1)}(z_{li}^{(1)}) , \\ g(\mu_i) = \eta_i^{(2)} &= \alpha^{(2)} + \sum_{m=1}^{M^{(2)}} \beta_m^{(2)} x_{mi}^{(2)} + \sum_{l=1}^{L^{(2)}} f_l^{(2)}(z_{li}^{(2)}) , \end{aligned} \quad (4.18)$$

where logit denotes the link function between the linear predictor $\eta_i^{(1)}$ and the probability of absence π_i , and $g(\cdot)$ is an appropriate link for the mean of h .

An alternative to these models is given by hurdle models (Mullahy, 1986; Cameron and Trivedi, 1998), where data are assumed to follow a finite mixture of a degenerate distribution with all its mass at zero and a zero truncated discrete distribution. That is, unlike the zero inflated models, in hurdle models, all observed zeros come from the zero-degenerate distribution. Following the same notation of Eq. (4.17), a hurdle model can be expressed as follows:

$$p(y_i|\pi_i, \mu_i, \boldsymbol{\psi}_1) = \pi_i \delta_0 + (1 - \pi_i) h(y_i|\mu_i, \boldsymbol{\psi}_1) I_{[y_i > 0]} . \quad (4.19)$$

As in (4.18), the hurdle model is completed when linking π_i and μ_i with their corresponding linear predictors.

However, the response variable is not always a discrete variable. Semi-continuous processes like rain, plant coverage, chemical concentrations, etc., are measured in the $[0, \infty)$ interval having high proportions of zero values, and there are neither an appropriate probability distribution nor a transformation available to adequately fit them. To model this type of processes, an extension of hurdle models for continuous data is required (Aitchison, 1955; Quiroz et al., 2015). Again, data are modeled as two independent sub-processes, one determines whether the response is zero, and the other determines the intensity when the response is non-zero using a continuous well known distribution as the log-Normal or the Gamma (Stefánsson, 1996; Brynjarsdóttir and Stefánsson, 2004; Paradinas et al., 2018). In this case, hurdle models are defined as a finite mixture of a degenerate distribution with point mass at zero and a distribution with support on \mathbb{R}^+ . If h is a pdf of some parametric continuous distribution with support on \mathbb{R}^+ (e.g. Gamma, log-Normal or log-logistic), the hurdle model for y_i (now assumed to be a continuous distribution) has the same mixture density as in (4.19). Although there exist an extensive list of zero-inflated or hurdle models dealing with correlated discrete data in many fields (Agarwal et al., 2002; Ver Hoef and Jansen, 2007), this approach has not been widely used with continuous responses.

It is worth noting that all the models commented in this section are a mixture of two processes, and in almost all cases, they are modeled independently (Neelon et al., 2013; Balderama et al., 2016). However, generally both sub-processes are related: low intensities are linked to low probabilities of presence and vice versa. Shared component modeling (SCM) are a good tool to deal with it by combining information both from the two subprocesses (Paradinas et al., 2018).

5 Discussion

This paper has reviewed some of the statistical challenges that can arise when the distribution of the species is modeled using geostatistical or point-referenced data. In particular, after describing in detail data and methods commonly used to model species distribution, we have focused on complex issues and we have discussed how they can be solved using Bayesian hierarchical spatio-temporal models. Specifically, in this review we have focused on the Bayesian approach and the INLA methodology (Rue et al., 2009) as they have several benefits with respect to the classical geostatistical methods. INLA allows to perform complex models with a minimum computational effort while obtaining accurate estimates. Its importance in the context of SDMs can be even more appreciated with the appearance of the recent project `inlabru` which has been created to develop and implement innovative methods to model spatial distribution and change from ecological survey data (<https://sites.google.com/inlabru3.org/inlabru>). In addition, classical geostatistical methods typically overestimate their predictive accuracy by using plug-in estimations of parameters in their predictive equations. (Diggle

and Ribeiro, 2007). On the contrary, inference about uncertainty, based on the observations and models, is a byproduct of the model predictions when the Bayesian framework is employed.

However, some limitations can arise when the INLA approach is used. For example, INLA can not handle missing values in spatially structured covariates. This issue can be framed in the misalignment problem discussed in Section 4.3; this means that it could be overcome applying a two-stage or joint modeling approach that allows to predict the covariate values in the locations where they were not measured. As above mentioned, an alternative is the one proposed by Gómez-Rubio and Rue (2017) that, using a more general approach, deals with missing values in the covariates, based on fitting conditional latent Gaussian models where covariates are imputed using a Metropolis-Hastings algorithm.

We would like to remark that, due to space limitation, we did not fully review the several complications that can derive from the sampling process. Indeed, we have only focused on the preferential sampling problem (Diggle et al., 2010), which, as previously mentioned, refers to the possibility that the sample design is stochastically dependent on the studied process. Nevertheless, other types of sampling procedures could produce different issues that should be taken into account in the statistical analysis. For example, one of the most popular methods used in ecology to estimate an animal population's size is the capture-recapture method that involves to capture, mark and release an initial sample of individuals (Otis et al., 1978; McInerny and Purves, 2011). Subsequently, a second sample of animal individuals is obtained independently and it is noted how many of them in that sample were marked. To model this type of data, a feasible solution could be the implementation of Bayesian hierarchical N-mixture models described in Section 4.5, which are currently being developed in INLA (Meehan et al., 2017).

Finally, an important point to consider is that INLA is not the only computational approach to make inference for Bayesian spatio-temporal models. In the last years, other approaches that also enable to achieve accurate species distribution models results, such as **stan** (Stan Development Team, 2015; Monahan et al., 2017), have been widely used.

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