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Research article

Dealing with area-to-point spatial misalignment in species distribution models

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Species distribution models (SDMs) are extensively used to estimate species–environment relationships (SERs) and predict species distribution across space and time. For this purpose, it is key to choose relevant spatial grains for predictor and response variables at the onset of the modelling process. However, environmental variables are often derived from large-scale climate models at a grain that can be coarser than the one of the response variable. Such area-to-point spatial misalignment can bias estimates of SER and jeopardise the robustness of predictions. We used a virtual species approach, running simulations across different levels of area-to-point spatial misalignment to seek statistical solutions to this problem. We specifically compared accuracy of SER estimates and predictive performances, assessed across different degrees of spatial heterogeneity in environmental conditions, of three SDMs: a GLM, a spatial GLM and a Berkson error model (BEM) that accounts for fine-grain environmental heterogeneity within coarse-grain cells. Only the BEM accurately estimates SER from relatively coarse-grain environmental data (up to 50 times coarser than the response grain), while the two GLMs provide flattened SER. However, all three models perform poorly when predicting from coarse-grain data, particularly in environments that are more heterogeneous than the training conditions. Conversely, decreasing environmental heterogeneity relative to the training dataset reduces the predictive biases. Because predictions are made from covariate-grain data, the BEM displays lower predictive performance than the two GLMs. Thus, standard model selection methods would fail to select the model that best estimates SERs (here, the BEM), which could lead to false interpretations about the environmental drivers of species distributions. Overall, we conclude that the BEM, because it can robustly estimate SER at the response grain, holds great promise to overcome area-to-point misalignment.

Keywords: grain size, spatial misalignment, spatial resolution, spatial scale, species distribution modelling, species–environment relationships (SERs)



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Introduction

Since their emergence two decades ago (Guisan and Zimmermann 2000), species distribution models (SDMs) have been broadly used to guide management or conservation actions (Guisan et al. 2013). By estimating species–environment relationships (SERs), SDMs can characterise the suitable environmental conditions that management actions ought to maintain for effective conservation of any given species of interest (Greenwood et al. 2016). SDMs have also been used to predict species distribution ranges under both current and future environmental conditions and have therefore helped managers prioritise areas for conservation actions (Zurell et al. 2021). For such purposes, estimating SERs and associated species distributions at fine grains (i.e. high resolutions) is crucial (McPherson et al. 2006).

In the early literature, SDMs were mostly fitted with coarse-grain environmental covariates (Austin and Van Niel 2011), with the underlying assumption that species distributions are mainly driven by global or regional climate (Pearson and Dawson 2003). However, increasing amounts of highly resolved environmental data (Rebaudo et al. 2016) have demonstrated the importance of fine-grain environmental variability to explain species distributions (Meineri and Hylander 2017, Lembrechts et al. 2019). For instance, Ashcroft et al. (2009) highlighted the importance of fine-grain climate variability on the distribution of mountainous species. Similar studies conducted in forest systems revealed that canopy protection from sun radiation can buffer the effect of regional climate conditions by acting as a micro-refugia for some species (Zellweger et al. 2020, Stark and Fridley 2022). Hence, relying only on coarsely resolved environmental covariates in SDMs can produce a mismatch between the ecological grain, the grain at which the environment influences a species, and the analysis grain of covariate (hereafter covariate grain), the grain at which the environment is described by covariates (Potter et al. 2013, Lu and Jetz 2023). Note that the ecological grain, which corresponds to a spatial unit at which environmental variation can be considered negligible for the species, is a useful methodological concept but does not necessarily reflect true ecological processes. Mismatch between ecological and covariate grains might lead to misestimated SERs and low predictive power (Seo et al. 2009, McNerny and Purves 2011), particularly if the ecological grain is finer than the resolution of environmental covariates (Connor et al. 2018).

Ideally, ecological knowledge of the focal species should guide the choice of the relevant grains at which modellers incorporate the response and environmental variables in SDMs (Dormann 2007). Ecological processes affecting species distributions are inherently grain-dependent (i.e. a particular case of scale dependence; Sandel 2015). For instance, vegetation type can determine the presence of insects, small mammals and birds across a range of species-specific grains (from centimetres to kilometres). In this example, available vegetation data at a given grain are unlikely to be ecologically relevant for all three taxonomic groups. Unfortunately, grains

of underlying ecological processes are generally unknown before the design of monitoring programs (Fletcher et al. 2023). Moreover, SDM studies commonly rely on existing species and environmental data. Many species data used in SDMs come from previous scientific surveys (Zipkin et al. 2010), citizen science (e.g. Global Biodiversity Information Facility (GBIF); Faurby and Araújo 2018) or museum records (Marcer et al. 2012). Associated environmental covariates are often derived from gridded climate re-analysis product (e.g. WorldClim (Hijmans et al. 2005) or National Oceanic and Atmospheric Administration (NOAA) products (www.ncei.noaa.gov) for terrestrial and marine environments, respectively) or remote sensing data (Pettorelli et al. 2014). Thus, data availability may limit the choice of the response and covariate grains and lead to a grain mismatch between the response variable and covariates (Moudrý et al. 2023), a specific case of spatial misalignment (Gotway and Young 2002). There are two types of spatial misalignment that involve a grain mismatch between the response and environmental variables (Moudrý et al. 2023): 1) point-to-area misalignment, where the response grain is coarser than the covariate grain (e.g. when the species data are coarse-grain museum records, basically 5×5 km grid cells; Marcer et al. 2012) and 2) area-to-point misalignment, where the covariate grain is coarser than the response grain (e.g. when point-level species records are collected, typically through citizen science monitoring such as GBIF, and associated with gridded climate data; Austin et al. 2019). Readers dealing with point-to-area misalignment can refer to other works (McPherson et al. 2006, Keil et al. 2013, Šimová et al. 2019, Moudrý et al. 2023). Here, we will focus on area-to-point misaligned data, and in particular cases where the covariate grain is assumed to be coarser than the ecological grain (e.g. for sessile species; Lu and Jetz 2023).

Area-to-point misaligned datasets can be spatially matched by either upscaling or downscaling the grain of the response variable or covariates, respectively (Latimer et al. 2006, Keil et al. 2013). Upscaling methods (e.g. spatial thinning) can help match fine-grain response data with coarse-grain environmental data (Steen et al. 2021, Meynard et al. 2023). However, in cases where the ecological grain is finer than the covariate grain, upscaling induces information loss in fine-grain variability (McInerny and Purves 2011). Thus, analyses targeting fine-grain species distributions should privilege downscaling of environmental data rather than upscaling species data. However, even if methods for downscaling environmental data exist (Hewitson and Crane 1996), they are rarely applied in SDM-based studies (Manzoor et al. 2018). Thus, area-to-point misalignment is usually not considered when describing fine-grain species distributions, which implies that fine-grain species records within a coarse-grain grid are all associated with the same environmental value (Latimer et al. 2006). This 'naïve' downscaling becomes problematic when the covariate grain is coarser than the ecological grain. Such a situation, expected for species having a fine ecological grain (e.g. sessile species), or when using relatively coarse environmental data (Lu and Jetz 2023), can introduce errors in

model covariates and compromise SDM accuracy (McInerney and Purves 2011). For instance, considering environmental data at a grain coarser than the ecological grain implies that the observed environment is a smoothed (less variable) version of the environment experienced by the species (Fig. 1; Potter et al. 2013, Haesen et al. 2023). McInerney and Purves (2011) showed that such errors in covariates could flatten estimated SERs with consequences on model predictive performance. In addition, not considering fine-grain environmental heterogeneity is likely to induce spatial autocorrelation not captured by the coarse-grain covariates, thereby biasing SDM estimates (Dormann et al. 2007, Kneigt et al. 2010). These biases can then lead to poor predictions of species distributions (e.g. overestimation of species range; Connor et al. 2018) or biodiversity patterns (e.g. mis-estimation of multifaceted diversity; Chauvier et al. 2022), making

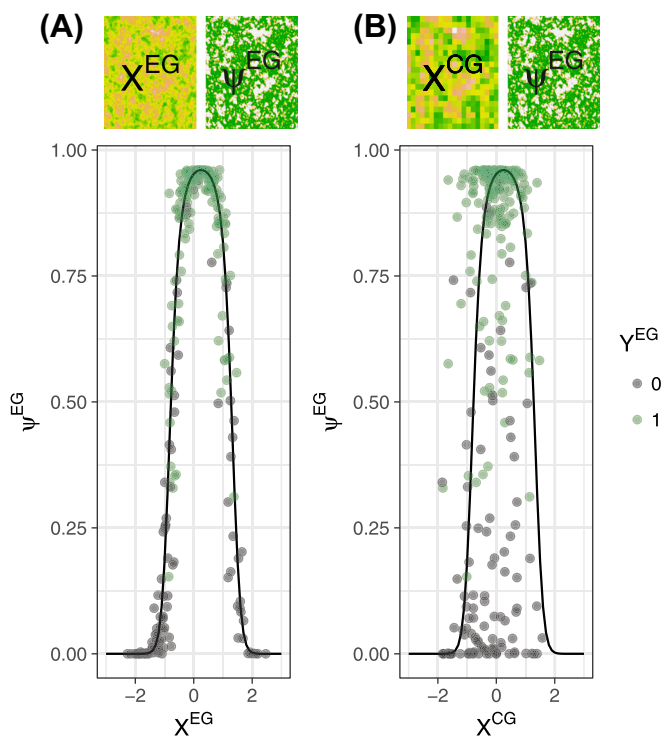


Figure 1. Illustration of area-to-point misalignment effect on simulated relationships between an explanatory variable (X) and species probabilities of presence (ψ). Left panel (A) represents a scenario with no misalignment, where species and environmental data are both sampled at the ecological grain (EG, grain at which the environment affects the species). Right panel (B) represents a scenario where the covariate is a gridded climate re-analysis product describing average environmental conditions at a given covariate grain (CG) coarser than the ecological grain at which species presence-absence (Y) are sampled. Superscripts indicate the grain at which the data are sampled. Black lines represent the true species-environment relationship used to simulate the probabilities of presence from the covariate at ecological grain. Points represent hypothetical samples of 300 locations from which environmental data have been extracted at (A) the ecological grain or (B) a coarser covariate grain. Note the difference of amplitudes in observed covariates (x -axis) between (A) and (B).

area-to-point spatial misalignment a common challenge in SDM-based studies (Martínez-Minaya et al. 2018).

Two types of models have previously been proposed to account for the fine-grain variability not described by coarse-grain environmental covariates (Martínez-Minaya et al. 2018): Berkson error models (BEMs; McInerney and Purves 2011) and point-level spatial GLMs (spGLMs; Latimer et al. 2006). BEMs and spGLMs account for unobserved fine-grain environmental variability in different ways. BEMs estimate SERs by fitting the response variable to an unobserved (error-free) covariate assumed to be more variable than the available (error-prone) covariate (Blangiardo and Cameletti 2015, Muff et al. 2015 for more details). Alternatively, spGLMs include a random spatial effect that accounts for unexplained fine-grain variability (Latimer et al. 2006). To our knowledge, the efficiency of these two models in accounting for area-to-point misalignment in SER estimates has not been thoroughly tested. Indeed, although McInerney and Purves (2011) investigated the ability of BEM to estimate SERs, they assumed a known variance error between the unobserved error-free and the observed error-prone environment. Yet, this information is not available for most climate data. In addition, spGLMs can improve explanatory or predictive power compared to non-spatial models when spatial heterogeneity remains unexplained by covariates (Dormann et al. 2007). However, to our knowledge, spGLMs have not been tested in the case of area-to-point misalignment.

In this study, we investigate how area-to-point misalignment, when environmental data are available at a coarser grain than the response and ecological grains, affects the performance of three alternative SDMs: a GLM (a frequently used SDM; Norberg et al. 2019), a spGLM and a BEM, which can both be relevant to address area-to-point misalignment (Latimer et al. 2006, Martínez-Minaya et al. 2018). We expect the problem of spatial misalignment not only to vary across models but also to increase with both increasing environmental heterogeneity, and coarsening of covariate grain (i.e. higher level of spatial misalignment). Relative to the GLM, the BEM and the spGLM are expected to more accurately estimate SERs (Latimer et al. 2006, McInerney and Purves 2011), but how well they can predict fine-grain species distributions using coarse-grain environmental data remains unclear. We ran simulations using a virtual species approach (Meynard and Kaplan 2013) to assess the performance of the three models regarding 1) SERs estimates and 2) predictive power in new environments across different levels of spatial heterogeneity and spatial misalignment.

Materials and methods

Terminology and data structure

Area-to-point misalignment describes the case where we observe a response variable (e.g. species occurrences, count, presence-absence) at N spatial point locations, while associated explanatory variables (e.g. environmental descriptors)

are available at a coarser grain, typically across a grid of I cells, each of which can contain multiple sampling points. Importantly, environmental variability is usually neglected within each cell where all points are assumed to share the same environment (Latimer et al. 2006). This leads to an area-to-point misalignment problem where the grain of the response variable is finer than the one of the predictor variable. We denote $Y_{j(i)}^{RG}$ the observed response variable (where RG stands for response grain) at sampling point j within grid-cell i , for $i = \{1, \dots, I\}$ and $j(i) = \{1, \dots, J_i\}$, with J_i the number of sampling points in grid-cell i and $\sum_{i=1}^I J_i = N$ the total number of sampling points. Let X_i^{CG} be the value of the available covariate (where CG stands for the covariate grain) within grid-cell i for any sampling point $j(i)$, and $X_{j(i)}^{RG}$ be the true (or error-free) value of the environmental variable at sampling point $j(i)$ within grid cell i (i.e. at the RG). In the case of the area-to-point misalignment described in this study, $X_{j(i)}^{RG}$ is unobserved and assumed to drive ecological processes (species distribution in this case). As such, the response grain is considered as equal to the ecological grain (denoted EG ; i.e. the grain at which the ecological process takes place). Note that this case of area-to-point misalignment can be extended to cases where the response variable is observed at a grid level (i.e. not necessarily points) with a finer resolution than the CG .

Simulation study

We ran simulations using a virtual species approach (Meynard and Kaplan 2013), where the species distribution depends on a single covariate, to test the effect of area-to-point spatial misalignment on the explanatory and predictive performance of the three models. The virtual species approach allowed us to know the true ecological process generating the observed data and thus estimate the true accuracy of the models. It also helped to distinguish the effects of area-to-point misalignment from other unknown sources of uncertainty inherent in real ecological data. The simulation design, represented in Fig. 2, consisted of three steps: 1) a data generating step replicated 30 times using a known underlying SER and three sizes of covariate grain to simulate 90 training datasets subject to three different levels of area-to-point misalignment, 2) a model fitting step where the three models were fitted to the different training datasets for a total of 270 models and 3) a model evaluation step to assess the ability of models to explain, interpolate and extrapolate probabilities of species presence at the ecological grain.

We simulated a grid of 1000×1000 points representing a virtual sampling area. The grain of this grid, the point level, was next considered as the ecological grain (EG). We simulated the virtual environment as a Gaussian spatial random field using a Matérn covariance matrix to represent spatial dependencies between spatial units. We set the spatial range (ρ), i.e. the distance at which the spatial correlation is close to 0.1 (Lindgren et al. 2011), and variance (σ^2) parameters of the Matérn function to 50 units and 1,

respectively. From these point-level environmental values (i.e. covariate values at the ecological grain X_j^{EG}) we calculated virtual probabilities of presence at the point level (i.e. at the ecological grain, ψ_j^{EG}) using a quadratic linear relationship: $\psi_j^{EG} = \beta_0 + \beta_1 X_j^{EG} + \beta_2 X_j^{EG^2}$. We chose the coefficients ($\beta_0 = 3$, $\beta_1 = 1.5$, $\beta_2 = -3$) to describe a sharp bell-shaped SER. We then simulated species presence-absence at the point level, Y_j^{EG} , using random draws from a Bernoulli distribution with parameter ψ_j^{EG} .

In the virtual observation process, we coarsened the resolution of the point-level environment by a factor 5, 25 or 50 corresponding to three different covariate grains (fine, medium or coarse), respectively. The environment at grid level was generated by averaging point-level environmental values comprised within each grid cell ($X_i^{CG} = \frac{1}{J_i} \sum_{j(i)=1}^{J_i} X_{j(i)}^{EG}$).

We chose the three grain sizes as fractions of ρ the environmental spatial range ($\rho/10 = 5$, $\rho/2 = 25$, $\rho = 50$). By doing so, we assumed that the effect of area-to-point misalignment depends on a ratio between the covariate grain and the environmental spatial heterogeneity (Gotway and Young 2002, Naimi et al. 2014). Indeed, we expect a greater loss of information when coarsening the covariate in heterogeneous environments (low spatial range ρ) than in homogeneous ones (high spatial range ρ) (Guo et al. 2023, Lu and Jetz 2023).

We then virtually sampled the simulated survey area by randomly selecting 300 sampling points. We simulate no bias in species sampling (i.e. perfect detection). Observed presence-absence data were thus equal to those simulated at the ecological grain (i.e. $Y_j^{RG} = Y_j^{EG}$). At each sampling point j , the observed covariate corresponds to the grid-level environment (i.e. for any point j within grid cell i : $X_{j(i)}^{CG} = X_i^{CG}$). We replicated the virtual sampling process 30 times, resulting in 90 simulated datasets (3 response grains \times 30 replications). The three models were fitted on each dataset (i.e. 90 training datasets and 270 fitted models). To evaluate the predictive performance of the models, we also simulated three different types of test datasets. First, to evaluate interpolation, we randomly sampled 300 new points within the same environment as for training datasets. To evaluate extrapolation, we simulated two new grids of 1000×1000 points X_{new1} and X_{new2} where the environmental conditions were more homogeneous or more heterogeneous relative to the training datasets, with an associated spatial correlation range of environmental values five times larger for X_{new1} ($\rho_{X_{new1}} = 250$) and five times smaller for X_{new2} ($\rho_{X_{new2}} = 10$). For both new environments, the same generating process as for the training dataset was applied, producing known probabilities of presence, presence-absence data and covariate values at the three covariate grains.

Modelling framework

Three models were considered: a generalized linear model (GLM), a spatial GLM (spGLM) and a Berkson error model (BEM). We fitted these models on presence-absence data,

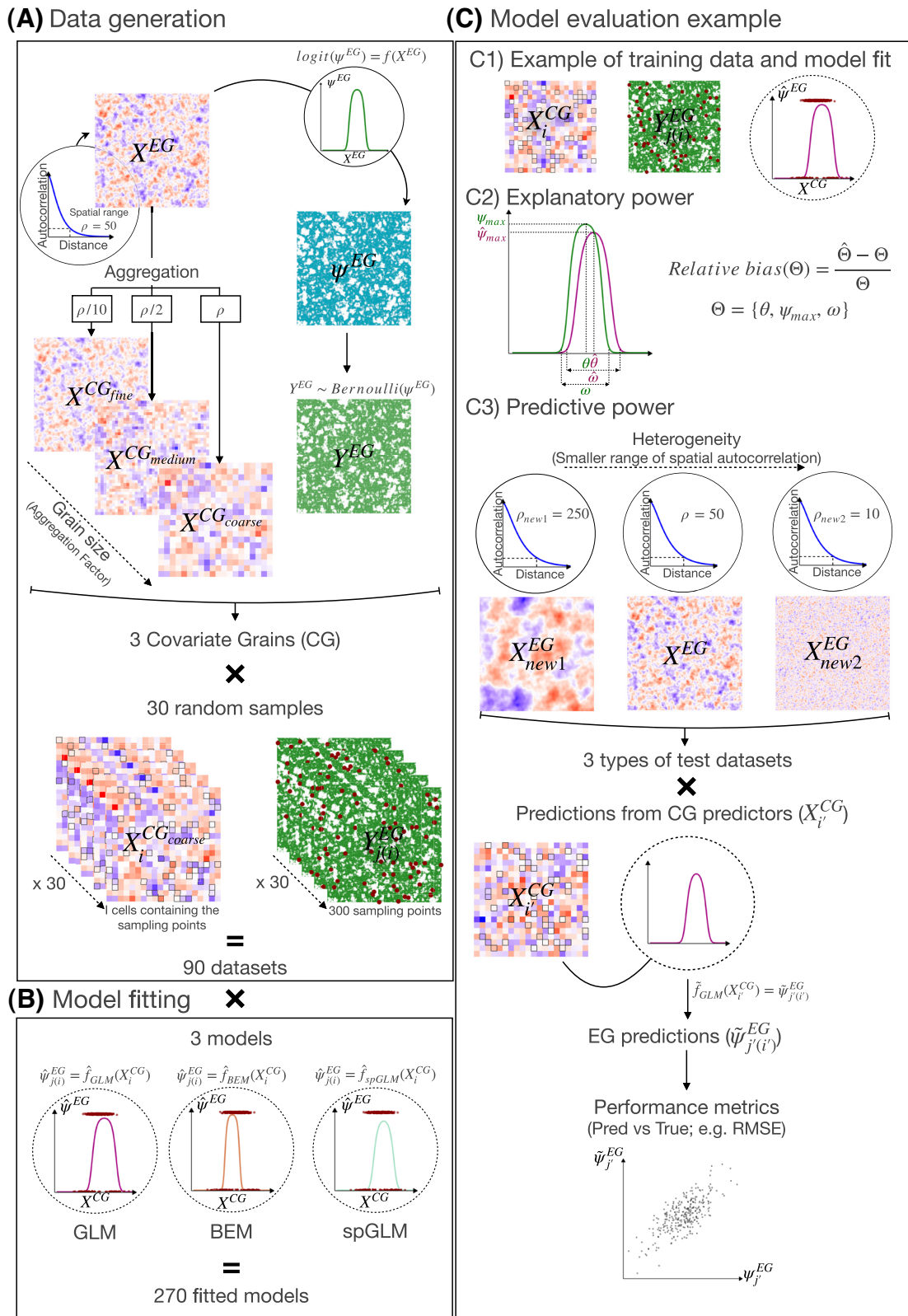


Figure 2. Representation of the simulation study designed to quantify the effect of area-to-point misalignment on the explanatory and predictive performance of three models. The design consists of three steps: (A) a data generation step, replicated 30 times, creating 90 simulated datasets containing point-level presence–absence data and gridded-environmental data from a known species–environment relationship (SER) and three covariate-grain sizes coarser than the response and ecological grains; (B) a model fitting step in which the three models were fitted to the area-to-point spatially misaligned datasets, resulting in 270 model fits; and (C) a model evaluation step in which, for each

Figure 2. Continued.

replicated combination of covariate grain size and model type (C1), was assessed: the accuracy of SER estimates (C2) and the ability of the models to predict ecological-grain species distribution from covariate-grain environmental data in areas with varying degrees of spatial heterogeneity (C3). EG = ecological grain (grain at which species experiences its environment); CG = covariate grain (grain of the covariate used to fit the models); BEM = Berkson error model; spGLM = point-spatial GLM; ψ = probability of presence; RMSE = root-mean-square error.

but note that these models can be fitted to other response variables (e.g. detection/non-detection, count, presence only). All models assume that the response variable $Y_{j(i)}^{\text{EG}}$ at sampling point $j(i)$ included in cell i relies on the probability of presence $\psi_{j(i)}^{\text{EG}}$: $Y_{j(i)}^{\text{EG}} \sim \text{Bernoulli}(\psi_{j(i)}^{\text{EG}})$. Each model makes specific assumptions about the relationship between the probability of presence and the environment. We fitted all models using scaled covariates (with mean 0 and SD 1). For simplicity, we present the formulation of the various models using one misaligned covariate, but this can be extended to more covariates.

The GLM considers that the environment at the covariate grain (i.e. the grid level), X_i^{CG} , is the only driver of variation in the probability of presence at the point level. In other words, the GLM assumes that the covariate grain is equal to the ecological grain. Thus, the SER is modelled as:

$$\text{logit}(\psi_{j(i)}^{\text{EG}}) = \beta_0 + \beta_1 X_i^{\text{CG}} + \beta_2 X_i^{\text{CG}^2}$$

where β_0 is the species probability of presence on the logit-scale in average environmental conditions (i.e. when the scaled covariate is null), and β_1 and β_2 are the coefficients representing the linear and the quadratic effects of environmental covariate X^{CG} , respectively. Note that we used a logit-link function as we modelled presence-absence data, but other link functions can be used depending on the type of data considered (e.g. a log-link function can be used for count data modelled with a Poisson or negative binomial distribution).

The spGLM is a mixed model that incorporates a spatial random effect, $\gamma_{j(i)}$, that allows variability between spatial points within a given covariate-grain grid cell. This spatial random effect allows the capturing of spatial signals not explained by the predictors (Zurell et al. 2021). For example, unobserved spatial patterns could result from missing spatially coherent or biological predictors (e.g. dispersal ability). Here, the spatial random effect is supposed to capture variability at the ecological grain, within each covariate grain cell. It is assumed that the probability of presence not only depends on the covariate grain environment (as for the non-spatial GLM) but also varies depending on a latent spatial field. The model is written as:

$$\text{logit}(\psi_{j(i)}^{\text{EG}}) = \beta_0 + \beta_1 X_i^{\text{CG}} + \beta_2 X_i^{\text{CG}^2} + \gamma_{j(i)}$$

$$\gamma \sim \text{MVN}(0, \Sigma)$$

where γ is a vector of dimension N , Σ is the spatial covariance structure whose generic element is

$\Sigma_{u,v} = \sigma_\gamma^2 \times \text{Matern}(d_{u,v}, \kappa)$ where σ_γ^2 is the variance component, $\text{Matern}(\bullet, \bullet)$ is the Matérn function which describes how the correlation between two points (here u and v) decreases with the Euclidean distance separating them (denoted $d_{u,v}$), and where κ is a scaling parameter related to the spatial range ρ , i.e. the distance at which the spatial correlation between two points is close to 0.1. It can be derived from κ by: $\rho = \frac{\sqrt{8\nu}}{\kappa}$, with ν representing the degree of smoothness of the spatial process and is usually fixed to one (Zuur et al. 2017).

The BEM jointly estimates the covariate and probability of presence at the point level (i.e. the ecological grain). It considers that the observed environment at the grid level X_i^{CG} is a smoothed version of the environment at the finer ecological grain $X_{j(i)}^{\text{EG}}$, which is assumed to be the 'true' driver of species distribution. This latent variable is modelled as:

$$X_{j(i)}^{\text{EG}} \sim N(X_i^{\text{CG}}, \sigma_X^2)$$

with σ_X^2 the variance parameter that describes the fine-grain variability lost by averaging the environment at coarser grains. The probability of presence is modelled as a function of the latent variable $X_{j(i)}^{\text{EG}}$:

$$\text{logit}(\psi_{j(i)}^{\text{EG}}) = \beta_0 + \beta_1 X_{j(i)}^{\text{EG}} + \beta_2 X_{j(i)}^{\text{EG}^2}$$

Parameter estimation

We fitted the GLM and the BEM within a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling with the R package 'nimble' (de Valpine et al. 2017, www.r-project.org). We ran three chains for each analysis with a burn-in of 10 000 and an additional 200 000 iterations with a thinning rate of 50. For prior distributions of parameters β_1 and β_2 , we used normal distribution with a zero mean and a precision of 0.1. For the intercept, β_0 , we specified a prior distribution on a derived ecologically meaningful parameter, $\psi^* = \exp(\beta_0) / (1 + \exp(\beta_0))$, representing the species probability of presence in average environmental conditions. We used a uniform prior bounded between 0 and 1 for this derived parameter, assuming no prior knowledge on species distribution patterns in average environmental conditions. We used half-Cauchy prior (Gelman et al. 2013) for the SD parameter in the BEM (σ_X). We assessed convergence by examining the Gelman-Rubin statistic (\hat{R}) with a threshold fixed to 1.1 (Gelman et al. 2013).

We fitted the spGLM using the INLA and SPDE approaches using the R package 'R-INLA' (Rue et al. 2009,

Lindgren et al. 2011). The ‘big n problem’ in spatial analysis, i.e. the computational challenge that arises when using a large amount of spatial data, prevented us from using MCMC samplers (Kery and Royle 2021). We used R-INLA’s default priors for the regression coefficients. We assigned a fixed shape ($\nu = 1$), and penalized complexity priors for the spatial range ρ and marginal SD σ_y , such that $\Pr(\rho > 1) = 0.05$, and $\Pr(\sigma_y > 5) = 0.05$. The mesh was constructed to allow fine-grain variability by specifying a maximum edge length of 10, smaller than the spatial environmental range.

Model performance assessment

We evaluated the models’ performance by investigating their ability to 1) infer the simulated SER (i.e. the explanatory power at the ecological grain), 2) predict species distribution in new locations of the study area (i.e. their predictive power with regard to interpolation) and 3) predict species distribution in new environments (i.e. their predictive power with regard to extrapolation, also called model transferability; Yates et al. 2018). Regarding 2) and 3), predictions were made from covariate grain data because in practice, although the aim is to estimate the SER and predict species distribution at the ecological grain, this grain is usually not available (otherwise, one would just use these data for model fitting). Yet, we also evaluated the models’ predictive power from ecological-grain covariate. Since results were similar to the ones related to 1), we here only present results associated with estimates of SER.

Regarding explanatory power, we calculated the relative bias regarding three parameters (Fig. 2, C1) describing the SER (Supporting information): the maximum probability of presence (ψ_{\max}), the environmental optimum (θ ; i.e. the environmental value associated with ψ_{\max}) and the width of the SER at a specified probability threshold of 0.05 (ω ; i.e. a measure of the species ecological tolerance). We also evaluated explanatory power by computing discrimination and calibration metrics that do not require knowledge of the true SER, as is the case in real case studies. To assess model discrimination (i.e. model ability to distinguish between occupied and unoccupied sites) we calculated the area under the receiver operator characteristic curve (area under the curve, AUC). To assess model calibration (i.e. model accuracy with regard to predicted probabilities of presence) we calculated Brier’s score (Brier). Brier assesses the mean squared error between predicted probabilities of presence and observed presence–absence, thus lower values are better (Liu et al. 2011). Both metrics were calculated by comparing observed presence–absence used to fit the models to probabilities of presence predicted from observed environmental values by the fitted models.

To evaluate the predictive power of the three models, we compared simulated probabilities of presence (i.e. true values, $\psi_{j'}$) with those predicted from the covariate grain environmental values by the fitted models (denoted $\tilde{\psi}_{j'}$). These comparisons were conducted for the three types of test datasets: the one used to evaluate the interpolation ability of the models and the two used for assessing extrapolation capacity

of models in more homogeneous or heterogeneous environments. We measured average accuracy of models to predict species probabilities of presence by calculating the root-mean-square errors (RMSE) as:

$$\text{RMSE} = \sqrt{\frac{1}{N'} \sum_{j'=1}^{N'} (\psi_{j'} - \tilde{\psi}_{j'})^2}$$

where $\psi_{j'}$ is the true probability of presence at site j' , $\tilde{\psi}_{j'}$ is the predicted probability of presence (i.e. the mean of the posterior distribution) and N' is the number of prediction points. Low values indicate a higher accuracy. We also computed prediction interval scores (PIS; see Eq. 43 in Gneiting and Raftery (2007)) that evaluate precision and coverage of credible intervals of predictions by penalizing large intervals and intervals that do not include the true value, with high values indicating poor predictive performance. As for explanatory power, we also computed discrimination (AUC) and calibration (Brier) metrics where predicted probabilities of presence were compared with observed presence–absence of the test dataset.

Results

Estimation of species–environment relationships

For all three models, biases in estimates of SER increased with increasing covariate grain sizes (i.e. decreasing covariate resolution), but responses varied across models (Fig. 3). The three models produced, on average, accurate estimates of optimum positions for all covariate grains; but variability among replicates of relative bias in optimum estimates increased with increasing grain size from 0.16 to 0.50 and from 0.16 to 0.49 for GLM and spGLM, respectively, and from 0.16 to 0.64 for BEM. For the three models, both underestimating maximum probability of occurrence, and overestimating ecological width, increased with covariate grain size, leading to flatter SER estimates (Supporting information). BEM produced the smallest bias, with a mean negative relative bias in maximum probability estimates of -0.03 (SD = 0.02) and a mean positive relative bias in ecological width estimates of 0.05 (SD = 0.11) at the coarsest resolution. In comparison with the BEM at the coarsest grain size GLM and spGLM produced relative bias 7.3 and 6.7 times larger, respectively, for maximum probability; and relative bias 7.6 and 7.0 times larger, respectively, for ecological width.

Performance metrics comparing observed presence–absence with predicted probabilities of presence from environmental covariate grain data indicated a decrease in explanatory power of the three models with increasing covariate grain size (Fig. 4, Supporting information). However, in contrast with previous results, these performance metrics suggested a lower explanatory power of the BEM than the spGLM at all covariate grain sizes with regard to both model calibration (higher Brier scores for the BEM) and discrimination (lower AUC values for the BEM). The GLM had equivalent discrimination power as the BEM and better calibration

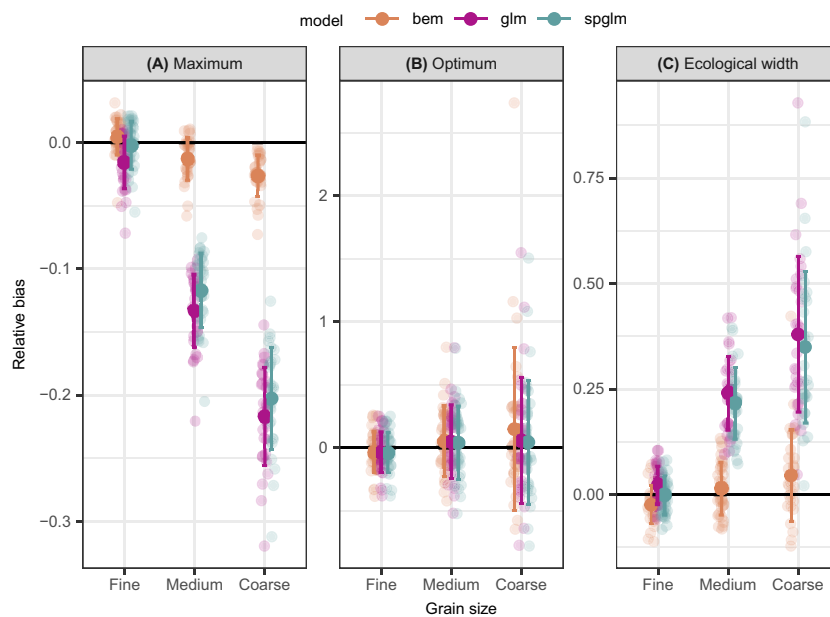


Figure 3. Ability of the three models (BEM, Berkson error model; GLM, generalized linear model; spGLM, spatial GLM; colour-coded on the graph) to infer the simulated species–environment relationship when fitted to environmental covariate at three grain sizes coarser than the ecological response grain. Relative biases between simulated and estimated values were calculated for three parameters describing unimodal species–environment relationships: (A) maximum probability of presence, (B) environmental optimum and (C) ecological width. Shaded points represent bias for each of the 30 simulated training datasets. Filled points represent the average bias among all training datasets while the vertical bars represent the associated SDs.

power, with lower Brier scores when fitted with covariates at medium and coarse grain sizes.

Predictive performance

Predictive performance of all models, in terms of both interpolation and extrapolation, decreased with increasing covariate grain size and spatial heterogeneity (Fig. 5, Supporting information). The lowest predictive performances were obtained when fitting models at the coarsest covariate grain while predicting in more heterogeneous environmental conditions than the training set. The three models had similar discrimination ability (Fig. 5 first row) for all covariate grains and types of test data, though variations were observed depending on calibration metrics. Since Brier and RMSE produced similar results we only present results from the former (see Supporting information for RMSE results). Different results were obtained with the PIS. Brier indicated equivalent predictive abilities for GLM and spGLM for both interpolation and extrapolation, regardless of environmental heterogeneity. In comparison, when fitted with medium and coarse covariate grains, BEM had lower predictive abilities when interpolating or when extrapolating in more heterogeneous conditions, whereas it performed slightly better in homogeneous environments. GLM had the worst PIS in all scenarios and was the most negatively affected by misalignment, because it tended to produce predictive intervals not including the true value that were too confident (Supporting information). The BEM and spGLM produced equivalent PIS in the case of interpolation. However, spGLM was better at predicting ecological grain species distribution from

environmental covariate grain data in a more heterogeneous environment for all covariate grain sizes, while BEM was better at predicting in a more homogeneous environment for all covariate grain sizes.

Overall, for the majority of simulated scenarios, we found lower predictive performance with regard to calibration metrics for the BEM than for the two GLMs when predicting probabilities of presence at ecological grain from environmental values at covariate grain (Fig. 5). This result may seem in contrast with the results above, indicating that the BEM accurately estimated SER (Fig. 3). This can be explained by the differences between the observed SER at the covariate grain, which relies on a truncated description of the environmental conditions experienced by the species, and the true SER at the ecological grain (Fig. 1). In contrast, although the two GLMs less effectively infer the true SER, their predictive performance outcompete the BEM because, by essence, these models do not aim to estimate the true SER (at the ecological grain) but rather the observed SER at the covariate grain, which directly advantages them when predicting from data at the covariate grain. However, because BEM better estimated SER at the ecological grain than the GLMs, it better predicted probabilities of presence at ecological grain from ecological grain environmental data (Supporting information).

Discussion

In this study, we evaluated the effect of area-to-point spatial misalignment between predictor and response variables (i.e. mismatch between a covariate grain and a finer response grain)

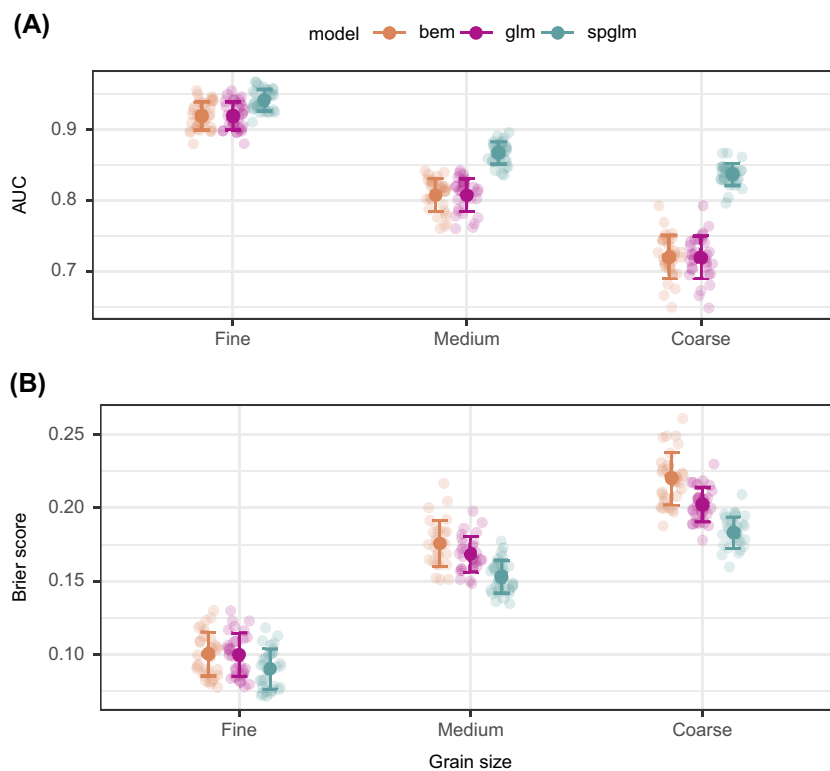


Figure 4. Explanatory performances of the three models (BEM: Berkson error model, GLM: generalized linear model, spGLM: spatial GLM) fitted with simulated point-level presence–absence data (i.e. at ecological grain) and grid-level covariate resolved at different grain sizes coarser than the ecological response grain. Model performance was evaluated with regard to (A) discrimination and (B) calibration power by comparing the point-level presence–absence with the predicted point-level probabilities of presence from grid-level environmental values. Filled points represent mean performance metrics over the 30 simulated training datasets (shaded points) while vertical bars represent the associated SDs.

on the performance of alternative SDMs. We specifically compared explanatory (i.e. estimates of SER) and predictive powers of three SDMs, namely: a BEM, a GLM and a spatial GLM (spGLM). For this purpose, we 1) simulated one SER at the ecological grain using a virtual species approach, 2) fitted the three models across three covariate grain sizes (coarser than the ecological grain) and finally 3) tested spatial predictions across different degrees of spatial heterogeneity in environmental conditions. We demonstrate that the BEM accurately estimates SER with an average bias ~ 7 times smaller than for the GLM and the spGLM, which both estimate flattened SERs. Despite its better estimates of SER, the BEM predictive performance is lower than those of the two other models because predictions are evaluated using covariate-grain data. However, BEM would outperform other models if evaluated using ecological-grain data (Supporting information), which are unfortunately rarely available for model evaluation in practice. Finally, the predictive power of all models decreases with an increase in either area-to-point spatial misalignment or spatial heterogeneity in environmental conditions.

As expected, area-to-point misalignment implies a loss of information, leading to an erroneously smoothed environment (Fig. 1, Supporting information). This error in covariates, known as the regression dilution problem, leads GLMs to estimate flattened unimodal SER (McInerny and

Purves 2011). Conversely to the GLMs, we show that the BEM, which accounts for the regression dilution problem, accurately estimates ecological-grain SER when fitted with a coarse-grain covariate. Thus, the BEM can help overcome area-to-point misalignment, as previously highlighted (McInerny and Purves 2011). Here, we show that specifying the degree of error in covariates (i.e. the degree of fine-grain environmental heterogeneity within coarse-grain cells) is not necessary for the BEM to accurately estimate the ecological-grain SER. This extends previous knowledge (McInerny and Purves 2011) and widens its potential range of application for species distribution modelling. For instance, for SDMs that combine both coarse-grain and fine-grain datasets to overcome niche truncation issues (Chevalier et al. 2021), the BEM can help refine SER estimates obtained from the coarse-grain dataset to improve predictions of fine-grain species distributions (Pacifi et al. 2019). Nevertheless, we implemented a BEM that assumes a constant error in covariates across grid cells (i.e. spatial stationarity; Dormann et al. 2007), which may not be a reasonable assumption in certain cases, especially in broad-extent studies or in areas where spatial heterogeneity strongly varies (e.g. mountains). Hence, while this study is a first step to account for area-to-point misalignment, additional research is needed to investigate how various factors can affect model performance. Specifically, future studies

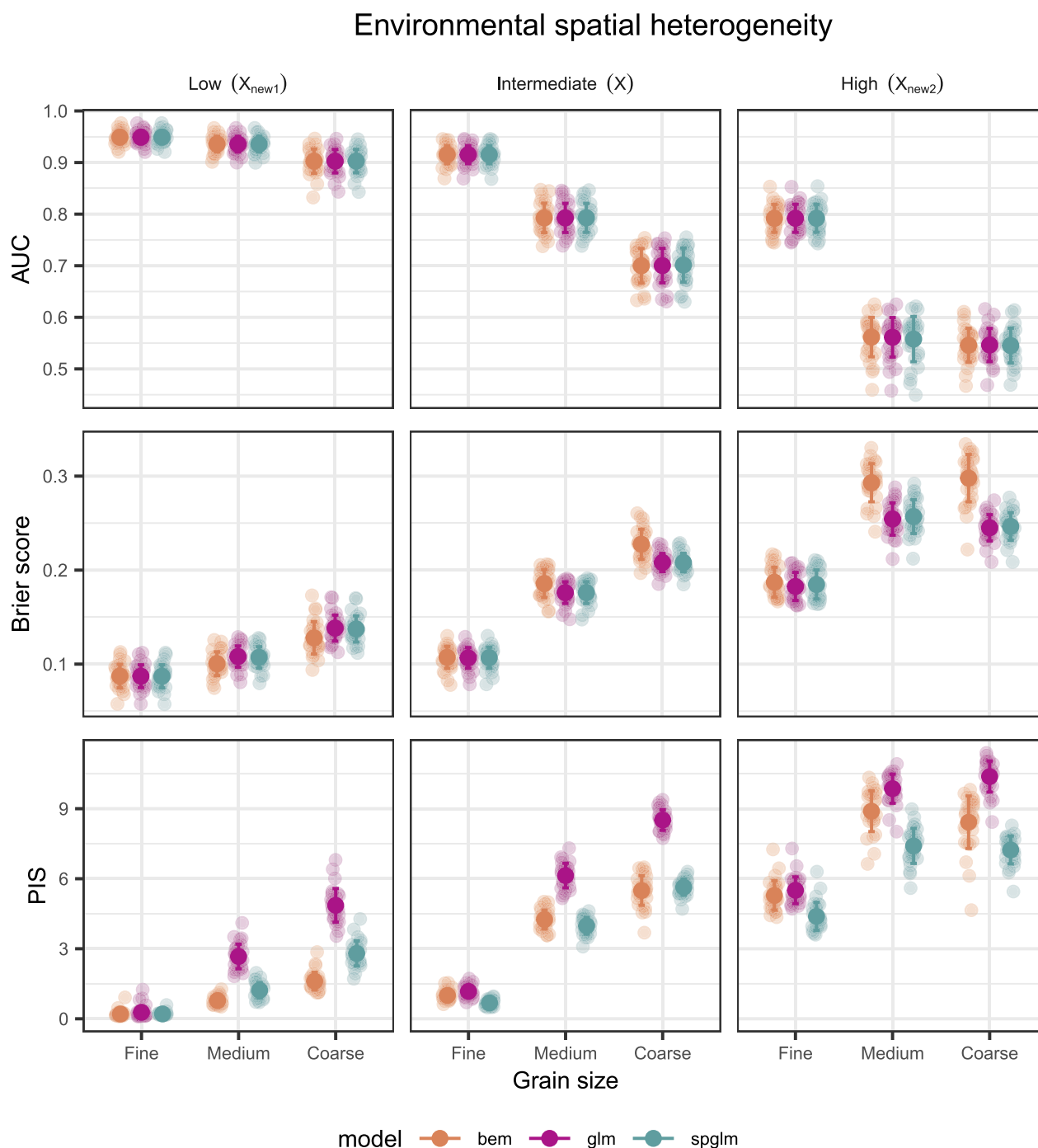


Figure 5. Evaluation of predictive performance of the three models (BEM: Berkson error model, GLM: generalized linear model, spGLM: spatial GLM) fitted with a misaligned covariate at three covariate grains coarser than the ecological grain with regard to their ability to predict species distribution at the ecological grain from environmental values at the covariate grain across three levels of environmental spatial heterogeneity (the three columns). The 2nd column informs on the models' interpolation ability with predictions performed at a random set of locations selected within the same environment as the training set. The 1st and 3rd columns inform on the models' extrapolation ability with predictions performed at a random set of locations selected within a more homogeneous environment (1st column) or a more heterogeneous environment (3rd column) than the one used to simulate training datasets. Performance metrics were computed by comparing predicted probabilities of presence at the ecological grain when fitting models at different covariate grains (fine, medium, coarse) against observed presence-absence (1st and 2nd rows) or simulated probabilities of presence (3rd row) at the ecological grain. Different colours correspond to different models with respect to colour code in the previous figures (orange for the BEM, purple for the GLM and green for the spGLM). Filled points represent mean performance metrics over the 30 simulated training datasets (shaded points) while vertical bars represent the associated SDs. PIS, prediction interval score; AUC, area under the curve.

ought to enhance the ecological realism of the current simulation framework by, for instance, considering: 1) additional covariates (potentially with different ecological grains or spatial heterogeneity), 2) different shapes of SER (i.e. varying beta coefficients), 3) various species prevalence and/or sample sizes (because of their effects on estimates of model parameters and associated confidence intervals; [Bazzichetto et al. 2023](#)), 4) additional modelling techniques (e.g. machine learning) or 5) spatial non-stationarity in covariates. How these various factors, which are known to affect SDM performance (e.g. generalists are less predictable than specialists; [Tessarolo et al. 2021](#)), interact with the problem of area-to-point spatial misalignment still requires dedicated investigation. Nevertheless, we can expect: 1) spatial non-stationarity in covariates to affect the performance of the BEM and spGLM; 2) a more acute area-to-point misalignment problem for specialists (i.e. species with sharp SERs) due to a higher probability of missing important environmental conditions with coarse-grain covariates ([Connor et al. 2018](#), [Lu and Jetz 2023](#)) and 3) machine learning algorithms to accurately estimate covariate-grain SERs, but to suffer from data overfitting in the context of area-to-point misalignment and to have limited transferability ([Yates et al. 2018](#)).

For the three models, predictive power (both calibration and discrimination) decreases with increasing magnitude of area-to-point spatial misalignment. This problem is magnified as spatial environmental heterogeneity in environmental conditions increases, which induces greater loss of information at the covariate grain (Supporting information). While this synergistic effect seems intuitive, a common practice in SDMs consists in coarsening predictors – regardless of spatial heterogeneity – to reduce the effect of positional errors in response variables (i.e. inaccurate geo-referencing of occurrence records; [Gábor et al. 2022](#)). However, recent evidence shows that coarsening of the predictors does not necessarily overcome the problem of positional errors ([Gábor et al. 2022](#)) but might actually transform one misalignment problem (point-to-point; [Naimi et al. 2014](#)) into another (area-to-point; [Connor et al. 2018](#)). The corollary is that an increasing number of studies might involve area-to-point misalignment. Our results indicate that BEM and spGLM can help account for area-to-point misalignment, under certain circumstances. For instance, while spGLM and GLM predictions are overall comparable, the spGLM better characterises prediction uncertainty by explicitly accounting for residual spatial autocorrelation ([Dormann et al. 2007](#)). Likewise, the BEM only outperforms the GLM when predicting in a smoother environment than this used for model fitting. Conversely, it performs poorly when predicting in equally or more heterogeneous environments (than this used for model fitting). Measurement error models, including BEMs, are not expected to perform better than GLMs when predicting from error-prone predictors ([Stoklosa et al. 2015](#)), due to a discrepancy between the grain at which SERs are estimated (i.e. covariate grain for the GLM but response grain for the BEM) and the grain at which predictions are made (i.e. covariate grain). However, in new environments

with different spatial heterogeneity, the magnitude of area-to-point spatial misalignment may vary ([Mertes and Jetz 2018](#)), making the GLM-estimated SER inappropriate for prediction in the new environmental conditions. In contrast, the BEM will perform well when predicting in environmental conditions that match the ones experienced by the species.

While the predictive and explanatory performances of the three models vary with the level of area-to-point misalignment, they do not reflect differences in the accuracy of SER estimates. For instance, performance metrics suggest a better explanatory power for the spGLM than the BEM. Similarly, the two GLMs present a better predictive power than the BEM. These counterintuitive results (knowing that the BEM better estimates the SER) emerge from evaluating predictions using covariate-grain data. Hence, a classic model selection framework would fail to select the model that best estimates the SER. This does not pose problems to predict at the covariate grain under similar environmental conditions (i.e. using an estimated SER that matches the prediction grain). However, if the aim is to predict under new environmental conditions (e.g. in the future or in a new area), the BEM would be less subject to extrapolation issues because of a more accurate estimation of the realised SER. For instance, when predicting in a different context (e.g. using fine-grain environmental data obtained from remote sensing in the same area; or extrapolating to an area with a different level of spatial heterogeneity), the two GLMs are likely to perform poorly, as their estimated covariate-grain SERs may underrepresent the whole range of conditions experienced by a species, unlike the BEM. Failure to select the model that best estimates the SER due to area-to-point misalignment may also lead to inaccurate ecological interpretations and inappropriate conservation recommendations. For instance, in our example, following a model selection framework would have resulted in selecting the spGLM, interpreting results based on a flattened SER and thus drawing incorrect conclusions about specific climatic tolerances, drivers of species distributions or climate-driven effects on spatial ranges ([Mertes and Jetz 2018](#), [Haesen et al. 2023](#), [Lu and Jetz 2023](#)). We therefore recommend caution when selecting models based on their predictive performance, especially for ecological interpretations, unless there is evidence (e.g. from the literature) that the covariate grain matches the ecological grain. For instance, birds or large mammals usually display spatially extensive home ranges, for which the use of coarse-grain climatic data may not be a problem. Conversely, SDM users should take great care when modelling species for which micro-environmental conditions might be important ([Chavier et al. 2022](#), e.g. sessile or specialist species; [Haesen et al. 2023](#)) or when conducting studies in highly heterogeneous environments (e.g. mountains or coastal areas).

By refining estimates of the SER at a grain that matches the ecological grain (i.e. the grain at which ecological processes act on species), the BEM can help better predict species distributions and the effect of climate change on species range. However, studies are needed to better understand the range of applicability of the BEM depending on various factors (e.g. spatial heterogeneity, multivariate cases) before it can be used

by managers and stakeholders to define conservation strategies. Furthermore, since the predictive ability of models are rarely assessed at the ecological grain, traditional evaluation metrics will fail at identifying the model that best estimates the true ecological-grain SER. This issue represents a great challenge given that most niche-based studies (e.g. niche overlap, niche conservatism, niche shift) assume that the estimated SER matches the ecological-grain SER. A first step toward preventing this issue would be to better understand how differences between measurement error models (e.g. BEM) and traditional models (e.g. GLM) can help characterise the magnitude of the mismatch between covariate and ecological grains.

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Author contributions

Bastien Mourguiart: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Mathieu Chevalier:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (lead). **Martin Marzloff:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Nathalie Caill-Milly:** Supervision (equal); Validation (equal); Writing – review and editing (equal). **Kerrie Mengersen:** Conceptualization (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (supporting). **Benoit Liquet:** Conceptualization (supporting); Methodology (supporting); Supervision (lead); Validation (equal); Writing – review and editing (equal).

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Data availability statement

R scripts for generating the data and reproducing the analyses are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.8239229> (Mourguiart et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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