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Research Article

Keywords: Global scale, INLA, non-stationary effects, spatio-temporal distributions

Posted Date: September 15th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10928856/v1>

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Additional Declarations: No competing interests reported.

Towards spatio-temporal analysis of global species distribution models

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Abstract

Species distribution models (SDMs) have been widely applied at regional scales; however, there is a growing need to extend these models globally in order to capture the large-scale environmental and ecological processes that drive marine species distributions. With the aim of moving toward more realistic global marine SDMs, this study presents a novel approach for global species distribution modeling by automating the integration of spatio-temporal barriers and spherical meshes within the Integrated Nested Laplace Approximation and Stochastic Partial Differential Equation framework. By constructing a global mesh using

spherical coordinates and anisotropic covariance structures, we ensure biologically realistic connectivity across ocean basins. A user-friendly interactive **RShiny** application is presented to facilitate the creation and tuning of global barrier polygons and spherical meshes. We assess the capabilities of this approach through a comprehensive simulation study and two case studies, where we analyze the spatial and temporal distribution of Atlantic cod (*Gadus morhua*) and reef-building corals (*Scleractinia*).

Keywords: Global scale, INLA, non-stationary effects, spatio-temporal distributions

1 Introduction

Forecasting complex global marine spatio-temporal species distributions requires integrating ecological processes and models capable of representing connectivity patterns across the world's oceans. This involves addressing several methodological challenges, including the representation of spatio-temporal dependence, the incorporation of physical barriers that restrict connectivity among ocean basins, and the need to account for the spherical geometry of the Earth. As these models become increasingly sophisticated, there is also a growing need for practical and accessible tools that facilitate their implementation and allow researchers to apply advanced methodologies without extensive technical development. The following sections review these challenges and introduce the framework proposed in this study.

1.1 Global marine Species Distribution Models

Species distribution models (SDMs) are widely used in ecology to understand spatial patterns and forecast species responses to environmental changes (Merow et al., 2014). By linking species data, such as species occurrences, abundance, or biomass, with environmental drivers such as sea surface temperature, salinity, or ocean currents, SDMs provide spatially explicit predictions of ecosystem dynamics (Zimmermann, Edwards Jr, Graham, Pearman, & Svenning, 2010). This allows us to assess the effect of climate change on species distributions, providing crucial information for conservation planning, ecosystem management, and biodiversity protection (Hoegh-Guldberg, Northrop, & Lubchenco, 2019). Furthermore, SDMs enable researchers to project future distribution changes, especially in the face of ongoing climate change (Austin & Van Niel, 2011; Stanton, Pearson, Horning, Ersts, & Reşit Akçakaya, 2012). In particular, marine species exhibit a greater tendency to shift their distributions in response to environmental changes compared to their terrestrial species (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019).

Traditionally, species distribution modeling efforts have focused on regional scales, providing valuable insights into biodiversity patterns and species' habitat preferences at the particular regional level analyzed (Pasanisi, Pace, Orasi, Vitale, & Arcangeli, 2024; Thompson, Couce, Schratzberger, & Lynam, 2023; Yen, Thomson, Vesk, & Mac Nally, 2011). However, as the impacts of climate change and other anthropogenic stressors generalize and intensify, there is an increasing need to complement regional

assessment with a more global perspective (Ready et al., 2010; Ringler et al., 2013; Tittensor et al., 2010). Global scale SDMs offer a complementary approach to regional models that allows to capture large-scale dynamics related to connectivity and the movement of marine species (Fuster-Alonso et al., 2025).

Global scale species distribution models have already been developed for marine species using different approaches. For instance, AquaMaps relies on expert-defined environmental envelopes (Kaschner et al., 2016), while other methods, such as those based on Bayesian Additive Regression Trees (BART), use machine learning to infer distributions from data (Cruz, Pennino, & Lopes, 2024; Fuster-Alonso et al., 2025).

Although these approaches have provided valuable information, they also have limitations. For instances, some of them do not account for spatial autocorrelation, which can lead to biased predictions due to the unmodeled spatial structure (Fuster-Alonso et al., 2024). Others do not incorporate ocean connectivity, assuming unrestricted movement across basins despite the presence of strong dispersal barriers such as landmasses. Precisely, on a global scale, continents act as major barriers to dispersal, reducing connectivity between ocean basins. These geographical constraints should be included in global models to produce realistic predictions of species distributions. Additionally, most of these models are constructed on flat, two-dimensional projections, which introduce distortions when applied to global, spherical surfaces. Overcoming these issues is essential to enhance the accuracy and ecological relevance of global marine SDMs.

1.2 Accounting for spatial dependence, barriers and spherical geometry

A very powerful and flexible way to incorporate the spatial autocorrelation in SDMs is considering them as hierarchical Bayesian spatial models (Banerjee, Gelfand, & Carlin, 2025; Hefley & Hooten, 2016; Martínez-Minaya, Cameletti, Conesa, & Pennino, 2018) and to use the Integrated Nested Laplace Approximation (INLA, Rue, Martino, & Chopin, 2009) and the Stochastic Partial Differential Equation (SPDE) approach (Lindgren, Rue, & Lindström, 2011) to make inference and prediction on them. But moreover, the INLA-SPDE approach can be extended to build global models that account for the spherical geometry of the Earth’s surface (Lindgren, Bakka, Bolin, Krainski, & Rue, 2024; Lindgren, Bolin, & Rue, 2022). The final challenge needed to develop global SDMs for marine species is accounting for the physical and ecological barriers that influence species movement. Again, the INLA-SPDE approach has also provided a statistical framework for addressing this challenge at regional level by incorporating non-stationary spatio-temporal dynamics into species distribution models (Bakka, Vanhatalo, Illian, Simpson, & Rue, 2019). Extending this regional approach to a global one can also be done, although it involves far more complex decisions about coastlines, narrow straits, artificial connections, and heterogeneous oceanographic pathways.

As the complexity of the data analyzed and the structure of the SDMs used increases, so does the difficulty of its implementation. As a result, there has been a recent interest in the development of various tools to facilitate the incorporation and use of complex data and new statistical methodologies, mostly embodied in new R packages and Shiny applications (Chang et al., 2026). These applications allow researchers

115 to build, visualize and validate complex models through intuitive interfaces, improving
 116 reproducibility and accessibility (see, for instance, [Figueira, Conesa, & López-Quílez, 2024](#);
 117 [Mestre-Tomás, Fuster-Alonso, Bellido, & Coll, 2025](#); [Moraga, 2017](#); [Osorio-Olvera et al., 2020](#)). Note that the final objective of these developments is to enable
 118 the integration of advanced approaches like INLA into broader modeling pipelines,
 119 bridging the gap between methodological innovation and practical implementation.
 120

121 1.3 Objectives and contributions of this study

122 In line with these challenges, we propose a novel framework to improve global marine
 123 species distribution models by integrating spatio-temporal barrier structures within
 124 the INLA-SPDE approach, while explicitly accounting for the spherical geometry of
 125 the Earth. Although barrier models and spherical SPDE meshes have been developed
 126 separately, their combined application on a global scale has remained largely unex-
 127 plored, and no practical framework currently exists to implement these models in an
 128 automated and accessible way for applications. Our approach enables spatial depen-
 129 dence to be modeled using geodesic distances while preventing unrealistic correlations
 130 across landmasses or disconnected ocean basins, thereby increasing the geographic and
 131 ecological realism of global SDMs. In addition, we provide an interactive **Shiny** applica-
 132 tion that facilitates the automated construction and tuning of global barrier polygons
 133 and spherical meshes, allowing researchers to explicitly define ecological connectivity
 134 across complex marine regions. Together, these developments provide a practical, flexi-
 135 ble, and computationally efficient framework for modeling marine species distributions
 136 at the global scale.

137 Regarding the structure of this paper, Section 2 introduces the methodological
 138 foundations of the proposed framework, including the formulation of spatio-temporal
 139 models using the INLA-SPDE approach on the sphere and the incorporation of bar-
 140 rier structures to represent restricted spatial connectivity. Section 3 describes the
 141 implementation of the global barrier model, including mesh construction, simulation
 142 of spatio-temporal random fields, and the generation of synthetic observations used
 143 to evaluate model performance. Section 4 presents the **Shiny** application developed
 144 to facilitate the construction and manipulation of global barrier polygons, providing
 145 an accessible interface for defining complex connectivity structures. In Section 5, we
 146 illustrate the proposed methodology through a simulation study designed to assess the
 147 behavior of the model under different response distributions. Finally, Section 6 presents
 148 two real-world case studies analyzing the spatio-temporal distribution of Atlantic
 149 cod (*Gadus morhua*) and reef-building coral (*Scleractinia*), followed in Section 7 by
 150 conclusions and implications of our findings for global species distribution modeling.

151 2 Global spatio-temporal INLA and barrier models

152 In what follows, we introduce the methodological framework proposed to construct
 153 global spatio-temporal species distribution models. We first describe the INLA-SPDE
 154 approach for modeling spatial and spatio-temporal dependence, highlighting its for-
 155 mulation on the sphere to properly represent global processes. We then present
 156 the extension of this framework to incorporate spatial barriers, which allows the

157 model to account for restricted connectivity caused by landmasses and other physi-
 158 cal constraints. Together, these components provide the methodological basis for the
 159 construction of ecologically realistic SDMs on a global scale.

160 2.1 Spatio-temporal models with INLA on the sphere

161 The Integrated Nested Laplace Approximation (INLA) has become a standard
 162 methodology for Bayesian inference in latent Gaussian models, particularly suited for
 163 spatial and spatio-temporal applications (Bakka et al., 2018; Blangiardo & Cameletti,
 164 2015; Rue et al., 2009). Here, we focus on how to model and analyze spatio-temporal
 165 geostatistical data, which assumes that observations are generated from a continuous
 166 spatial process evolving over time. Analyzing point pattern data could be done sim-
 167 ilarly by considering them as a realization of Log-Gaussian Cox Processes (Simpson,
 168 Illian, Lindgren, Sørbye, & Rue, 2016), as presented in Section 5.2.

169 In particular, if Y denotes the response variable and $y = (y_1, \dots, y_n)$ are the
 170 resulting observations of that response at locations $s = (s_1, \dots, s_n) \in \Omega \subset \mathbb{R}^2$, the
 171 geostatistical model is given by:

$$y_i \mid s_i \sim F(\mu_i, \phi), \quad g(\mu_i) = \mathbf{X}_i \boldsymbol{\beta} + \sum_j f_j(z_{ij}) + u(s_i), \quad (1)$$

172 where $F(\cdot, \phi)$ denotes the likelihood distribution (belonging to the exponential family)
 173 with dispersion or shape parameters ϕ ; $g(\cdot)$ is a suitable link function; $\mathbf{X}_i \boldsymbol{\beta}$ represents
 174 the linear predictor; and $f_j(z_{ij})$ are smooth or random effects of covariates z_{ij} . Finally,
 175 $u(s_i)$ represents the spatial random effect modeled as a Gaussian random field (GRF)
 176 with a Matérn covariance function:

$$\text{Cov}(u(s_i), u(s_j)) = \sigma^2 \frac{2^{1-\nu}}{\Gamma(\nu)} (\kappa \|s_i - s_j\|)^\nu K_\nu(\kappa \|s_i - s_j\|), \quad (2)$$

177 where ν is the smoothness parameter, $\kappa > 0$ is a scaling parameter related to the
 178 spatial range, σ^2 is the marginal variance, and K_ν is the modified Bessel function of
 179 the second kind.

180 A key advance in this framework is the integration of the Stochastic Partial Differ-
 181 ential Equation (SPDE) approach, which enables the approximation of the previous
 182 Gaussian random field by defining it as the solution to a stochastic partial differential
 183 equation. This yields to a sparse Gaussian Markov Random Field (GRMF), drastically
 184 reducing computational costs associated with high-dimensional latent fields (Lindgren
 185 et al., 2011).

186 In particular, the spatial component of the model, $u(s)$, is defined via the SPDE:

$$(\kappa^2 - \Delta)^{\alpha/2} u(s) = \mathcal{W}(s), \quad s \in \Omega, \quad (3)$$

187 where κ is that in equation (2), α determines the smoothness of the field, Δ is the
 188 Laplacian operator, and $\mathcal{W}(s)$ is spatial Gaussian white noise. For $\alpha = 2$, the solution
 189 $u(\mathbf{s})$ corresponds to a Gaussian random field with a Matérn covariance function that

190 can be scaled to have marginal variance σ^2 , with correlation range $r = \sqrt{8}/\kappa$ (Lindgren
191 et al., 2011).. The solution is discretized over a triangulated mesh using finite element
192 methods (FEM), yielding a GMRF with sparse precision matrix $\mathbf{Q}$ such that:

$$\mathbf{u} \sim \mathcal{N}(\mathbf{0}, \mathbf{Q}^{-1}), \quad (4)$$

193 where $\mathbf{u}$ is the vector of the latent field values at mesh nodes. This sparsity
194 enables scalable inference, particularly when combined with INLA’s nested Laplace
195 approximation.

196 Building on this spatial formulation, a spatio-temporal model generalizing that in
197 equation 1 by including observations during different instants of time t , can be obtained
198 by allowing the above mentioned spatial latent field to evolve over time. Rather than
199 treating each time point as an independent spatial surface, a temporal dependence
200 can be introduced so that the field at time t is linked to its previous states.

201 In particular, the spatio-temporal component of the model, $u(s, t)$, is defined via
202 the SPDE:

$$\frac{\partial u(s, t)}{\partial t} + (\kappa^2 - \Delta)^{\alpha/2} u(s, t) = \mathcal{W}(s, t), \quad (s, t) \in \Omega \times \mathbb{R}^+, \quad (5)$$

203 where $\mathcal{W}(s, t)$ is spatio-temporal white noise and the remaining parameters are as in
204 equation (2). This evolution equation assumes a separable continuous-time autore-
205 gressive process over space and is solved numerically using a tensor product structure
206 between spatial FEM basis functions and temporal basis functions. The discretized
207 model yields a sparse block-structured precision matrix, preserving computational
208 feasibility over large spatial domains and long time series.

209 Until recently, most applications of the INLA-SPDE methodology were based on
210 flat, two-dimensional projections that only partially represent the geometry of the
211 Earth. Recent developments have extended the INLA-SPDE framework to global
212 domains by defining spatial fields directly on the sphere $\mathbb{S}^2$ (Lindgren et al., 2024,
213 2011). In this setting, the SPDE in equation (3) is not approximated on a planar
214 projection, but on a triangulated spherical manifold, so that the finite element repre-
215 sentation respects the geometry of the Earth’s surface. In practice, this representation
216 is implemented through the `fmesh` library (Lindgren, 2026), which provides tools for
217 constructing spherical triangular meshes and for performing the finite element calcu-
218 lations required by the SPDE approach on curved manifolds. An additional advantage
219 is its ability to handle coordinate reference systems and transformations between geo-
220 graphic coordinates, the Earth’s surface, and the unit sphere used for modeling. This
221 makes it possible to represent global spatial dependence in a geometrically consistent
222 way while retaining the computational efficiency of the SPDE and GMRF framework.

223 Therefore, the INLA-SPDE framework provides a rigorous and computationally
224 efficient approach to spatio-temporal modeling. Using sparse GMRF approximations
225 and solving SPDEs over spherical domains, this methodology enables the construction
226 of high-resolution global models that preserve spatial structure, accommodate tempo-
227 ral dynamics, and remain computationally tractable even in large-scale ecological and
228 environmental applications.

2.2 Non-stationary spatial models and physical barriers

Traditional spatial models often assume that the underlying spatial process is stationary and isotropic. However, in many ecological applications, such assumptions fail to capture the true spatial dependence, particularly when physical barriers such as coastlines, peninsulas, islands or other bathymetric discontinuities restrict connectivity (Bakka et al., 2018; Krainski et al., 2018). These scenarios require more flexible models capable of incorporating non-stationary and anisotropic dependence structures.

In particular, Bakka et al. (2019) proposed a barrier model within the SPDE framework that modifies the spatial operator in regions where connectivity is restricted. The domain Ω is partitioned into two disjoint subdomains: Ω_n , corresponding to normal regions where spatial correlation is permitted, and Ω_b , corresponding to barrier regions where correlation is strongly reduced. The SPDE is then defined as:

$$u(s) - \nabla \cdot \left(\frac{r^2}{8} \nabla u(s) \right) = r \sqrt{\frac{\pi}{2}} \sigma_u \mathcal{W}(s), \quad s \in \Omega_n, \quad (6)$$

$$u(s) - \nabla \cdot \left(\frac{r_b^2}{8} \nabla u(s) \right) = r_b \sqrt{\frac{\pi}{2}} \sigma_u \mathcal{W}(s), \quad s \in \Omega_b, \quad (7)$$

where r and r_b are the spatial ranges in Ω_n and Ω_b , respectively, with $r_b \ll r$. Typically, r_b is chosen to be very small, so that spatial correlation is strongly suppressed across barrier regions. These modifications are incorporated through the finite element mesh and the local stiffness matrices, ensuring that the resulting precision matrix respects physical discontinuities while maintaining sparsity (Krainski et al., 2018).

Implementing spatio-temporal barrier models can be carried on both R-INLA (Lindgren & Rue, 2015) and `inlabru` (Bachl, Lindgren, Borchers, & Illian, 2019), which have complementary roles. While R-INLA provides the core engine for approximate Bayesian inference in latent Gaussian models and SPDE-based spatial effects, `inlabru` builds on this framework by offering a more user-friendly and flexible interface for model specification, prediction, and interpretation, particularly in geostatistical applications (see, for instance, Martino et al., 2021; Pace et al., 2022; Panunzi et al., 2025). Thus, R-INLA carries out the inference itself, whereas `inlabru` facilitates the practical implementation of complex spatial and spatio-temporal models. Still, the construction of the barrier structure must be addressed before inference and prediction can be performed.

Different studies have applied this barrier model to account for more realistic movement and dependence structures in spatial ecological applications: the distribution of fish larvae in the Finnish Archipelago (Bakka et al., 2019); the distribution of bottlenose dolphins (Martínez-Minaya, Conesa, Bakka, & Pennino, 2019); the spread of *Xylella fastidiosa* (Cendoya, Hubel, Conesa, & Vicent, 2022); the distribution of salinity in the Chesapeake Bay (Desjardins, Davis, & Curriero, 2024); the distribution of white sharks in the Mediterranean Sea (Panunzi et al., 2025); as well as in studies of estuarine debris, coastal fish biodiversity and community change, and water-quality dynamics in complex aquatic systems (Chaudhuri, Juan, Saurina, Varga, & Saez, 2023; Gacutan, Tait, & Clark, 2024; Jaksons, Bell, Jaksons, & Cook, 2022; Jónsdóttir,

Bakka, & Elvarsson, 2019; Nishimoto, Miyashita, & Fukasawa, 2024; Requena-Mullor et al., 2026).

Taken together, these studies have shown that barrier models can substantially improve spatial inference when movement or dependence is constrained by physical obstacles. In such settings, the main effect of the barrier is often clear: landmasses and coastal features prevent standard stationary models from inducing unrealistic dependence between nearby locations that are physically separated. Barrier SPDE models address this issue by restricting correlation across those obstacles, leading to spatial predictions that are more consistent with the underlying ecological or physical processes.

However, all those applications have been developed at regional or relatively localized scales, where barriers are easier to define and the structure of connectivity is more readily interpretable. Although extending this idea to the global ocean may seem conceptually straightforward, it involves substantial challenges from an implementation perspective. At planetary scale, coastlines are highly irregular, narrow straits may either restrict or permit connectivity, artificial channels can create unexpected links, and dispersal pathways are influenced by heterogeneous oceanographic conditions that vary across regions. As a result, defining barrier structures globally is not simply a matter of transferring regional methods to a larger map, but of developing a representation that remains both ecologically meaningful and computationally feasible over the entire sphere. As shown in the [barrier-global tutorial](#) (included in the official R-INLA repository), this requires a specific workflow to construct, edit, and validate global barrier polygons before they can be incorporated into the mesh and used in the spatio-temporal modeling framework.

3 MOBIE: a Shiny App for building global barriers

In order to facilitate the definition of global barrier structures, here we present MOBIE, an interactive **Shiny** application that allows users to build, upload, edit, visualize, and export global barrier polygons within a single workflow.

As it can be seen in panel A of Figure 3, the application includes a default global land barrier, created by dissolving country borders into a single polygon, but also allows users to upload their own barrier files in common spatial formats. This global polygon can be simplified, small isolated islands can be removed, and users can also manually refine the barrier by drawing polygons on the map and either adding them to or subtracting them from the current barrier. This makes it possible to adapt the barrier definition to the spatial scale and ecological assumptions of each analysis, especially in regions where narrow passages or local connectivity require explicit decisions. Panels B and C of Figure 3 show, respectively, examples of local polygon refinements used to control regional connectivity, and the final global barrier polygon.

In addition to polygon editing, the application also supports the construction of the spherical mesh used in the SPDE representation. Once the barrier polygon has been defined, users can generate a mesh directly on the sphere and classify mesh elements according to their position relative to the barrier. Mesh construction is controlled by two parameters: `mesh_globe_resolution`, which regulates the resolution

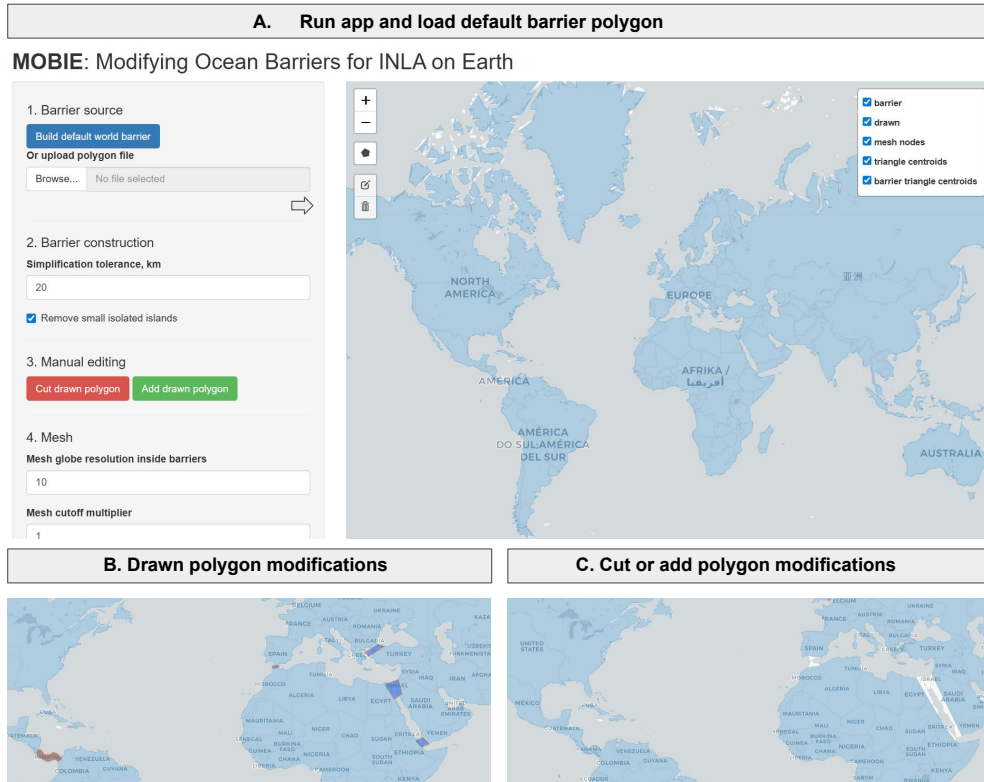


Fig. 1 Interactive **Shiny** interface for constructing and editing global barrier polygons. Panel A shows the application after loading the default global barrier polygon. The interface allows users to simplify the geometry, remove small isolated islands, and manually add or subtract drawn polygons from the barrier structure. Panel B shows examples of drawn polygons, and Panel C presents the resulting barrier modifications after applying the cut or add operations.

of the spherical mesh, and `mesh cutoff multiplier`, which controls the minimum separation between mesh nodes relative to the chosen resolution.

As shown in panel A of Figure 2, the resulting mesh nodes, triangle centroids, and barrier classified centroids can be displayed on the map, providing a direct visual check of the spherical mesh before model fitting. Panel B of Figure 2 presents detailed views of areas where mesh resolution and connectivity are especially important. Finally, panel C of Figure 2 shows correlation diagnostics from selected locations, confirming that spatial dependence is reduced across barrier regions while propagating coherently through the connected ocean domain.

The final barrier polygon can be exported as a **GeoJSON** file, while the mesh nodes and triangle centroids can also be downloaded for further inspection or use in subsequent modeling steps. This provides a reproducible pre-processing workflow in which both the barrier definition and the mesh construction are made explicit before the fitting process of the global SPDE barrier model (outlined in previous sections) starts.

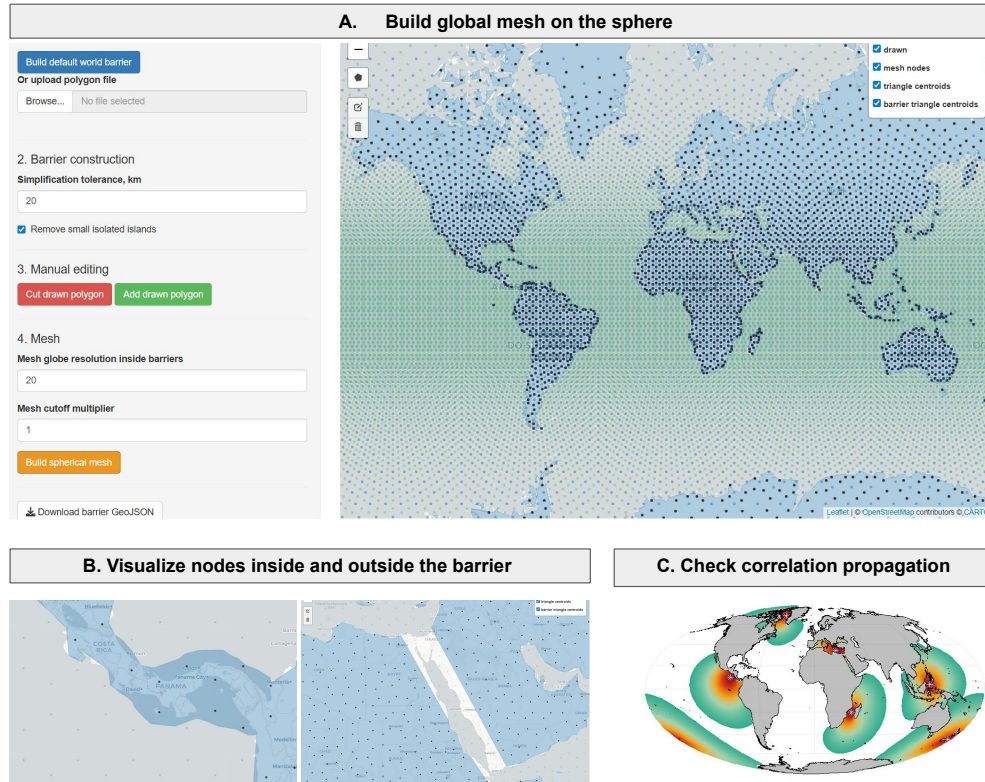


Fig. 2 Interactive Shiny interface for constructing the spherical mesh. Panel A shows the global mesh generated on the sphere together with mesh nodes. The interface allows users to control the mesh using the **mesh globe resolution** and **mesh cutoff multiplier** parameters. Panel B shows detailed examples of nodes classified relative to the barrier structure, and Panel C presents correlation propagation diagnostic for specific points across the global ocean domain.

4 Simulated species distribution scenarios

In this section, three examples are provided in order to illustrate the implementation of the global barrier formulation described in the previous sections in the context of marine species distribution modeling. The three examples use simulated data of increasing complexity, and were chosen to represent common data structures in ecological applications rather than as purely numerical validation exercises. The first one deals with a purely spatial Gamma model and it aims to represent positive abundance or biomass data. The second one is a spatio-temporal Gaussian model, representing continuous ecological or environmental responses observed repeatedly through time. In third place, we consider a spatio-temporal Bernoulli model, representing occurrence (presence-absence data), one of the most common response types in species distribution modeling.

Across the three scenarios, we assessed whether a global SPDE barrier model defined on the sphere could recover the main components of the data generating process while preserving biologically realistic ocean connectivity. In all cases, land masses were treated as barriers, spatial dependence was allowed to propagate through connected ocean regions, and selected narrow passages were preserved according to the global barrier definition. Bathymetry was included as a standardized covariate because it represents a key environmental gradient for many marine species and provides a realistic setting for evaluating fixed-effect recovery.

4.1 Spatial Gamma model with global barriers

Our first example deals with a purely spatial Gamma model that represents positive abundance or biomass data. In particular, a latent spatial field over the global ocean was simulated using the proposed global barrier model defined on a spherical mesh. As mentioned above, land masses were treated as barriers, so dependence spread through the ocean domain while being blocked across continents, except through explicitly preserved narrow connections.

In particular, the linear predictor of the model was set as:

$$\eta(s) = \beta_0 + \beta_1 x(s) + u(s),$$

where $u(s)$ is the latent spatial barrier field and $x(s)$ is a standardized covariate representing the bathymetry effect. The fixed effects were set to $\beta_0 = 1.2$ and $\beta_1 = -0.1$, so that deeper locations were associated with a smaller expected response on the log scale. The latent field was generated from a barrier Gaussian random field with marginal standard deviation $\sigma = 1$ and range parameter set to 4000 km in the main ocean domain, together with a much shorter barrier range of 50 km. The response was simulated using a Gamma distribution with mean $\mu(s) = \exp\{\eta(s)\}$ and shape parameter $\phi = 3$.

To assess parameter recovery, we repeatedly sampled 5000 observation locations 50 times from the same continuous Gamma simulated realization. In each repetition, a new set of ocean locations was drawn uniformly across the globe, and the corresponding response values were extracted from the simulated response surface. For each sampled dataset, we fitted a spatial Gamma model with a global barrier effect, including an intercept, a linear bathymetry effect, and a latent spatial component.

The results are summarized in Figure 3. Panel A shows the simulated realization of the latent spatial field generated under the global barrier model. Panel B presents the corresponding simulated realization of the continuous Gamma response surface obtained from the latent field and the bathymetry covariate. Panels C and D summarize parameter recovery across repeated samples. The posterior means of the fixed effects were centered close to their generating values, indicating that the model was able to separate the environmental effect from the latent spatial structure. The negative bathymetry effect was correctly recovered, and the spatial hyperparameters, including range and marginal standard deviation, were also estimated close to the true values.

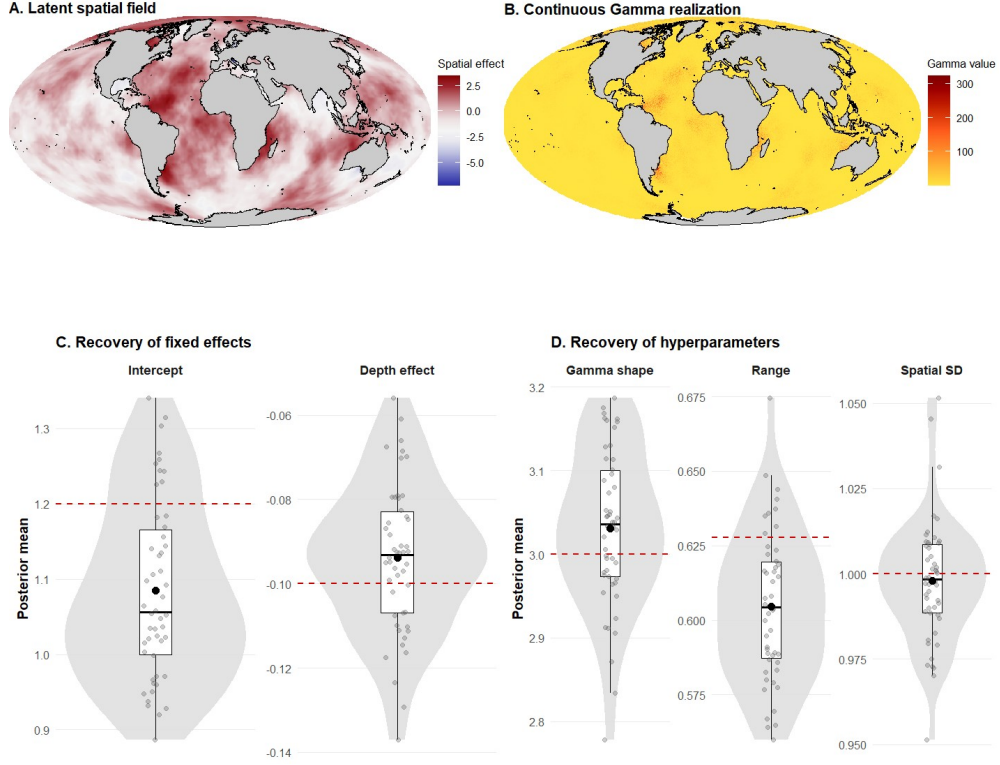


Fig. 3 Simulation illustration of the global barrier model for a spatial Gamma response. In panels C and D, points denote posterior means across repeated samples, boxplots summarize their distribution, and dashed red lines indicate the true values used in the simulation.

The variability among repetitions mainly reflects differences in the sampled locations, which is expected in global marine surveys where spatial coverage is often uneven. Overall, this scenario shows that the proposed model can recover fixed effects and spatial dependence for abundance-type SDMs while maintaining a realistic representation of marine connectivity.

4.2 Spatio-temporal Gaussian model

We now present a spatio-temporal example mimicking continuous environmental variables such as abundance or biomass. A latent spatio-temporal field over the global ocean considering physical land barriers was simulated, again allowing spatial dependence to propagate through ocean-connected regions while reducing unrealistic correlation across land masses.

The Gaussian model was set to

$$Y(s, t) \mid \mu(s, t), \sigma_e^2 \sim \mathcal{N}(\mu(s, t), \sigma_e^2),$$

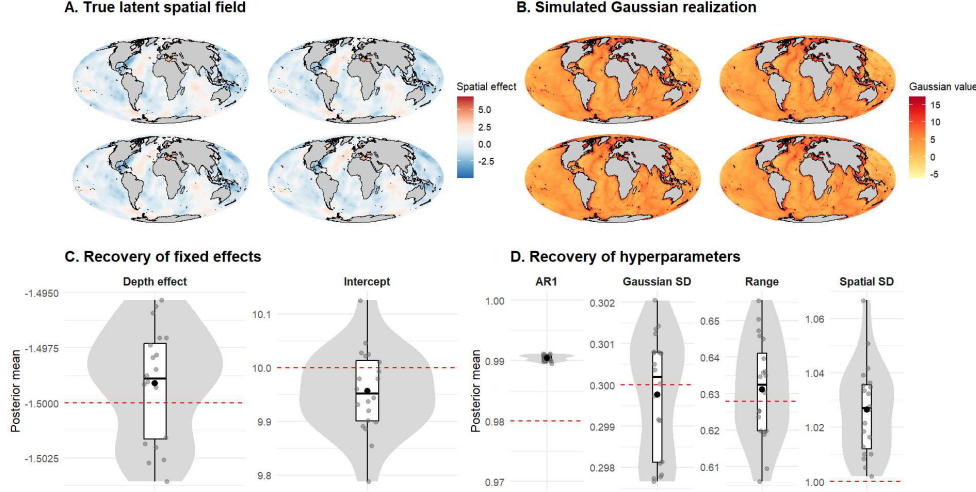


Fig. 4 Simulation-based illustration of the global barrier model for a spatio-temporal Gaussian response. In panels C and D, points denote posterior means across repeated samples, boxplots summarize their distribution, and dashed red lines indicate the true values used in the simulation.

being the linear predictor

$$\mu(s, t) = \beta_0 + \beta_1 x(s, t) + v(s, t),$$

with intercept $\beta_0 = 10$, depth effect (associated to the standardized bathymetry covariate) $\beta_1 = -1.5$, and Gaussian observation error standard deviation $\sigma_e = 0.3$. The latent spatial effect $u(s, t)$ was generated from the global barrier SPDE model with a spatial standard deviation of $\sigma = 1$ and practical ranges of 4000 km in the ocean domain and 50 km across barriers. Four temporal replicas ($k = 4$) were simulated to represent consecutive time periods, through an autoregressive structure of order 1 (AR1) being $\rho_{(AR1)} = 0.98$.

To assess parameter recovery, we repeatedly sampled 5000 observation locations 50 times from the same spatio-temporal Gaussian process. In each repetition, a new set of ocean locations was drawn for each time point, and the corresponding response values were extracted from the simulated field. For each sampled dataset, we fitted a spatio-temporal Gaussian model with a global barrier effect, including an intercept, a linear bathymetry effect, and a latent spatial component with an AR1 for the temporal component.

The results are summarized in Figure 4. Panel A shows the latent spatio-temporal field across the four time instants generated under the global barrier formulation. Panel B presents the corresponding Gaussian response surfaces. Panels C and D summarize recovery of the fixed effects and hyperparameters, including the spatial range, spatial standard deviation, Gaussian observation standard deviation, and AR(1) correlation. The posterior distributions remained close to the reference values, indicating that the model was able to recover the main components of the data-generating mechanism.

Some variability is expected because the simulation used a limited number of time points and different sampled locations in each repetition. Nevertheless, the results indicate that the proposed framework can model dynamic spatial distributions on the sphere, combining global ocean connectivity, environmental covariates, and temporal autocorrelation in a single coherent model.

4.3 Spatio-temporal Bernoulli model

We next considered a spatio-temporal Bernoulli response to mimic the probability of occurrence of a species based on presence-absence data over the global ocean. This is a particularly relevant setting for SDMs, since occurrence data are widely used when abundance information is unavailable. It is also a more challenging scenario than the previous case because binary observations contain less information about the underlying latent process. As in the Gaussian scenario, the latent process was defined through the proposed spatio-temporal global barrier model on a spherical mesh, with land masses acting as barriers that limited dependence across continents while maintaining connectivity through selected marine passages.

The occurrence model was set to

$$Z(s, t) \mid \pi(s, t) \sim \text{Bernoulli}(\pi(s, t)),$$

while the linear predictor was linked to the probability of occurrence $\pi(s, t)$ via the usual logistic function

$$\text{logit}(\pi(s, t)) = \beta_0 + \beta_1 x(s, t) + v(s, t),$$

with β_0 and β_1 set to 1 and -1.5 respectively. The latent spatial field was simulated using a global barrier SPDE structure with spatial standard deviation $\sigma = 1$ and practical ranges of 4000 km in the ocean and 50 km across barriers. Four temporal replicates ($k = 4$) were generated over time through an AR(1) temporal structure, where $\rho_{(AR1)} = 0.98$. Note that this latent effect $u(s, t)$ corresponds to the spatio-temporal barrier field, allowing occurrence probabilities to follow realistic oceanic connectivity patterns while limiting dependence across continental barriers.

Parameter recovery was evaluated by repeatedly sampling 5000 observation locations 50 times from the same spatio-temporal Bernoulli process. For each repetition, ocean locations were sampled independently at each time point, and binary responses were drawn from the corresponding occurrence probabilities.

The results are summarized in Figure 5. Panel A shows the true latent spatio-temporal field across the four time points, while Panel B presents the corresponding Bernoulli realizations used for sampling. Panels C and D summarize recovery of the fixed effects and hyperparameters. The posterior means remained centered close to the generating values, including the negative bathymetry effect. The spatial range, marginal standard deviation, and AR(1) temporal correlation were also broadly consistent with the values used in the simulation.

As expected, posterior variability was higher than in the Gaussian scenario, reflecting the lower information provided by binary data. Even so, results show that the

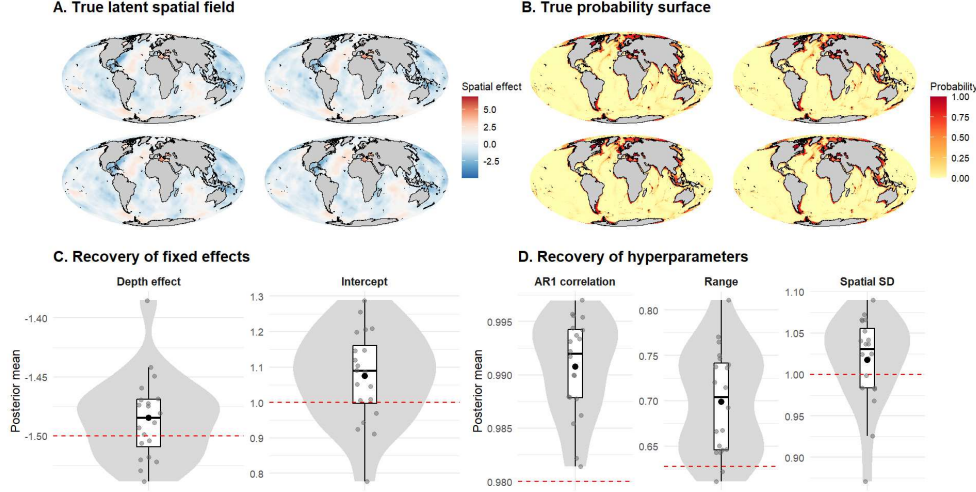


Fig. 5 Simulation-based illustration of the global barrier model for a spatio-temporal Bernoulli response. In panels C and D, points denote posterior means across repeated samples, boxplots summarize their distribution, and dashed red lines indicate the true values used in the simulation.

proposed framework can be applied not only to abundance or continuous responses, but also to occurrence data. This supports its use across different types of global marine SDMs.

5 Case studies

To illustrate the applicability of the proposed framework, we consider two complementary marine case studies. The first focuses on Atlantic cod (*Gadus morhua*) using standardized survey data obtained from the FishGlob database (Maureaud et al., 2021, 2024), while the second analyses reef-building corals of the order *Scleractinia* using global occurrence records from GBIF (GBIF, 2026). Together, both examples evaluate the proposed framework under different data structures, likelihoods, and ecological settings.

5.1 Atlantic cod

In the first case study, we analyze the spatial distribution of Atlantic cod (*Gadus morhua*). The database integrates standardized bottom-trawl surveys from multiple long-term monitoring programs and provides quality-controlled information on species occurrences, biomass, and Catch Per Unit Area (CPUA).

We employed CPUA as a proxy for abundance, using together all the spatial observations since the year 2000. Atlantic cod is a suitable case study because its distribution is associated with complex shelf systems in the North Atlantic, where geographic proximity does not necessarily imply ecological connectivity. Coastlines,

semi-enclosed seas, and narrow passages can strongly influence spatial dependence and should therefore be accounted for when modeling the species distribution.

In order to account for the large number of zero observations commonly found in marine survey data, we implemented a hurdle modeling framework (Paradinas, Conesa, López-Quílez, & Bellido, 2017) that separates the occurrence process from the positive biomass process. The first component models species occurrence using a Bernoulli likelihood, while the second component models positive biomass conditional on presence using a lognormal distribution. Both components include a spatial barrier effect defined on the sphere through the global SPDE framework.

In particular, the occurrence component is defined as:

$$\begin{aligned} Z_i \mid s_i &\sim \text{Bernoulli}(\pi_i), \\ \text{logit}(\pi_i) &= \beta_0^{(p)} + u_p(s_i), \end{aligned} \quad (8)$$

where Z_i denotes the presence-absence observation at location s_i , π_i is the probability of occurrence, and $u_p(s_i)$ is the latent spatial barrier field associated with the occurrence process.

Conditional on presence, the positive biomass component is modeled as:

$$\begin{aligned} Y_i \mid s_i, Z_i = 1 &\sim \text{Lognormal}(\mu_i, \sigma^2), \\ \mu_i &= \beta_0^{(b)} + u_b(s_i), \end{aligned} \quad (9)$$

where Y_i represents the positive CUPA value at location s_i and $u_b(s_i)$ is a latent spatial barrier field describing residual spatial dependence in biomass intensity. This spatial field could alternatively be shared or correlated with the spatial effect in the occurrence component, reflecting a possible link between the processes driving presence and biomass intensity.

The final hurdle prediction (Paradinas, Giménez, Conesa, López-Quílez, & Penino, 2022) was obtained by combining the posterior predictions from the two model components: the probability of occurrence and the biomass conditional on presence. This quantity represents the expected relative biomass under the hurdle process, where biomass is only expressed in locations where the species is predicted to occur. In this sense, the occurrence component acts as a probabilistic correction of the positive biomass component, reducing predicted biomass in areas with low probability of presence while retaining high values where both occurrence probability and conditional biomass are high. The result can therefore be interpreted as a hurdle-corrected prediction of relative biomass, integrating habitat suitability and biomass intensity.

Both spatial components were constructed using the global barrier SPDE model on a spherical mesh. The barrier polygon was adjusted with the RShiny application to better represent relevant marine connections and physical constraints in the study region. In this way, spatial dependence is propagated through connected oceanic pathways rather than across landmasses, producing predictions that are more consistent with the ecological structure of the North Atlantic and Arctic shelf systems.

Figure 6 summarizes the main results of the global analysis of this species. Panel (A) shows the predicted relative biomass conditional on presence, revealing high

505 biomass concentrations mainly along northern Atlantic shelf systems, particularly
 506 around the Northeast Atlantic, Iceland, and Greenland. Panel (B) presents the pre-
 507 dicted occurrence probability, identifying broader areas of environmental suitability
 508 across subarctic and temperate waters. Finally, panel (C) displays the hurdle-corrected
 509 relative biomass obtained by combining both model components. The final distribu-
 510 tion highlights a clear concentration of Atlantic cod biomass along productive shelf
 511 and coastal regions, while reducing predictions in offshore areas where occurrence
 512 probability is lower.

513 5.2 Reef-building corals

514 As a second case study, we analyze the global distribution of reef-building corals of the
 515 order *Scleractinia*. This group includes the main stony corals responsible for building
 516 tropical reef structures and is strongly associated with spatially complex marine habi-
 517 tats, including island systems, continental margins, and semi-enclosed tropical seas.
 518 These characteristics make *Scleractinia* a useful example to evaluate whether global
 519 barrier structures improve the ecological realism of spatial predictions.

520 Occurrence records were obtained from the GBIF database and filtered to retain
 521 observations with valid coordinates and reliable temporal information. Because GBIF
 522 data are presence-only and strongly affected by spatial and temporal variation in
 523 sampling effort, we modeled the records as a log-Gaussian Cox process (LGCP). This
 524 allows the observed point pattern to be represented as a spatial point process whose
 525 intensity varies continuously across the ocean.

526 In particular, if $\lambda(s)$ represents the intensity of the process at any location s of the
 527 ocean domain, then the probability of observing a certain number of locations observed
 528 in any area A of the ocean domain follows a Poisson distribution with intensity λ_A ,
 529 defined as:

$$\lambda_A = \int_A \lambda(s) ds. \quad (10)$$

530 The log-Gaussian Cox process arises from the fact that $\log(\lambda(s))$ can be modeled
 531 with a Gaussian linear predictor:

$$\log(\lambda(s)) = \beta_0 + u(s), \quad (11)$$

532 where β_0 is the intercept and $u(s)$ is a latent spatial Gaussian field defined on the
 533 spherical mesh.

534 In order to evaluate the effect of the barrier structure, we fitted two alternative
 535 models, being the first one the proposed global barrier SPDE, where landmasses act
 536 as barriers and spatial dependence is propagated through connected oceanic regions.
 537 The second model used a standard Matérn SPDE on the same spherical mesh, without
 538 barrier constraints. The log-intensity of both models can be written as:

$$\log(\lambda_B(s)) = \beta_0^B + u_B(s), \quad (12)$$

$$\log(\lambda_M(s)) = \beta_0^M + u_M(s), \quad (13)$$

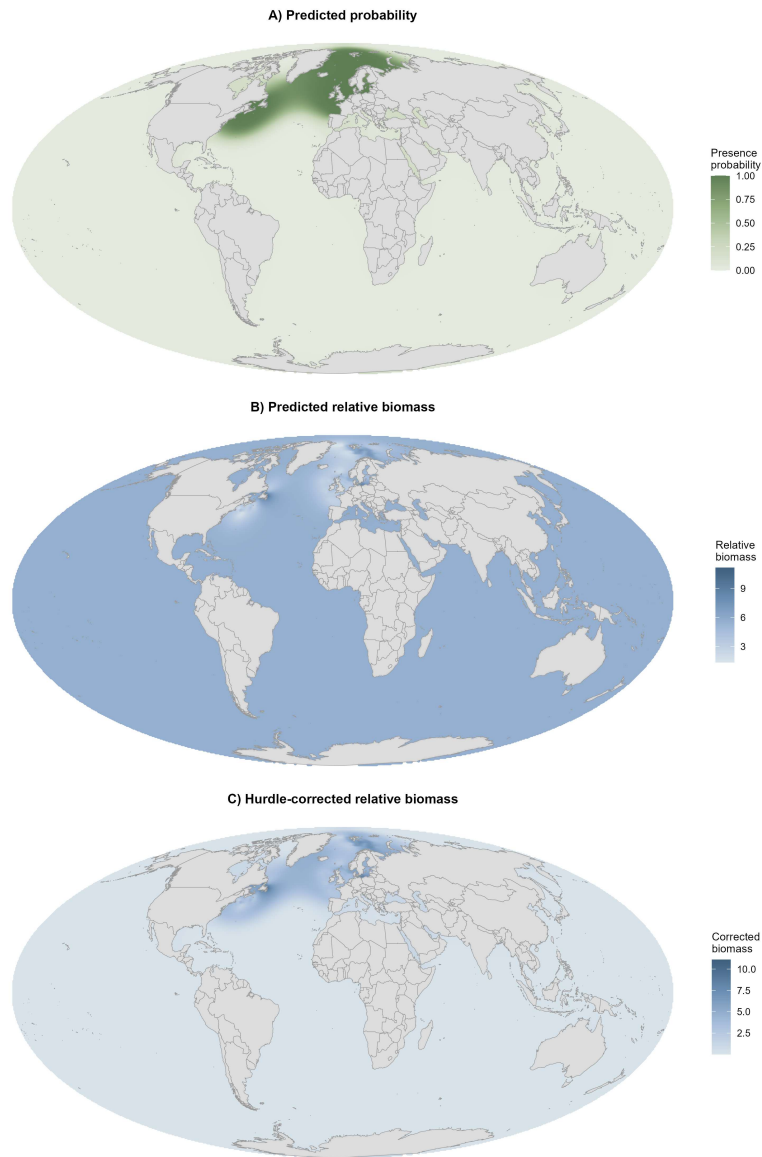


Fig. 6 Predictions obtained from the global hurdle barrier model for Atlantic cod (*Gadus morhua*). Panel A shows the predicted relative biomass conditional on presence based on the lognormal component of the hurdle model. Panel B presents the predicted occurrence probability estimated from the Bernoulli component. Panel C displays the hurdle-corrected relative biomass obtained by combining both model components.

where $u_B(s)$ denotes the spatial field estimated with the barrier model and $u_M(s)$ denotes the spatial field estimated with the standard Matérn model.

Predictions were obtained for both models over the global ocean domain. To compare the spatial patterns, we considered the predicted $\log(\lambda)$ intensity surfaces from the barrier and standard SPDE models and computed their spatial difference. Positive values indicate regions where the barrier model predicts higher relative intensity than the standard SPDE model, whereas negative values indicate regions where the standard model predicts higher relative intensity. This comparison provides a direct visualization of how restricting spatial dependence to connected marine pathways modifies the predicted distribution.

This comparison is not intended as a model-selection exercise, since the two models do not represent equally realistic assumptions. A standard spherical SPDE model allows spatial dependence to spread across landmasses and disconnected ocean basins, creating correlations that are not physically realistic in marine systems. In contrast, the barrier model restricts spatial dependence to connected marine regions and therefore produces predictions that are more consistent with real ocean connectivity. As a result, even if the unconstrained model shows similar or better information criteria, the barrier formulation provides spatial predictions that are more reliable with the physical structure of the ocean.

Figure 7 shows the predicted coral distribution obtained with the barrier and non-barrier models. The comparison highlights how the inclusion of global barriers modifies the spatial propagation of occurrence intensity across ocean basins, particularly around complex coastal and island systems. The difference map provides a direct visualization of where the barrier structure has the strongest effect on the predicted distribution.

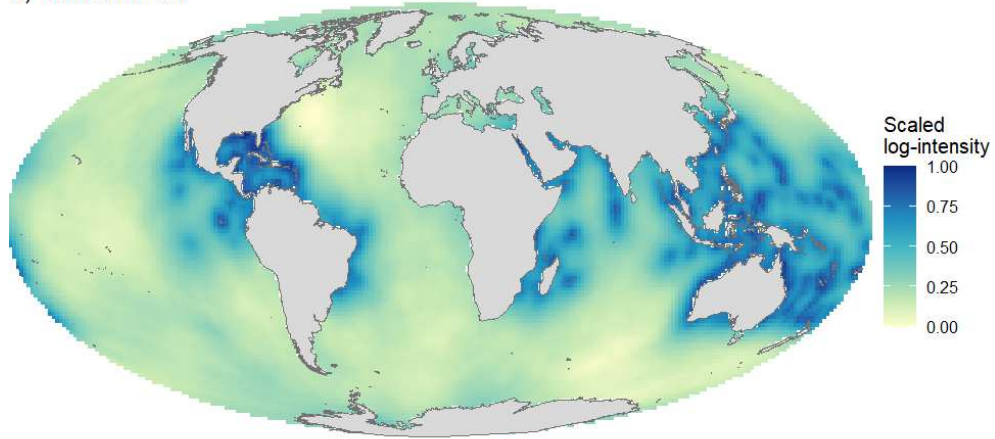
Overall, the coral case study demonstrates how the proposed framework can be used not only for prediction, but also to assess the influence of global barrier structures on species distribution models. By comparing models fitted on the same spherical mesh with and without barriers, we can identify where accounting for ocean connectivity changes the predicted spatial field and produces more interpretable global marine distributions.

6 Conclusions

In this work, we present a practical and automatic framework for incorporating global barrier structures into marine species distribution models using the INLA-SPDE approach on the sphere. The proposed methodology addresses two important limitations of many global SDMs: the geometric distortion introduced by planar projections and the unrealistic propagation of spatial dependence across land masses or disconnected ocean basins. By combining spherical meshes with barrier SPDE models, spatial dependence is allowed to propagate through connected marine pathways, leading to predictions that are more consistent with the physical and ecological structure of the ocean.

A central contribution of this work is the development of **MOBIE**, an interactive **RShiny** application designed to support the construction, editing, visualization, and export of global barrier polygons and spherical meshes. The application makes the

A) Barrier model



B) Difference in scaled log-intensity

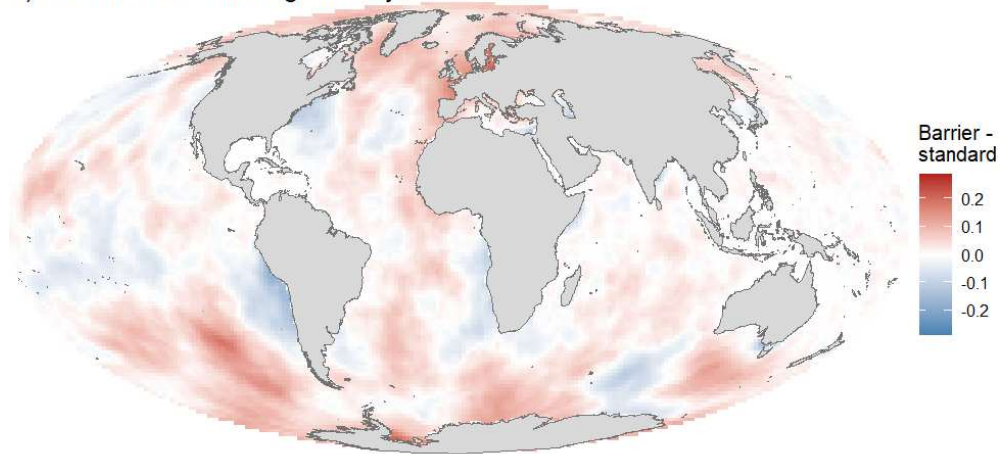


Fig. 7 Comparison between the global LGCP fitted with and without spatial barriers for reef-building corals (*Scleractinia*). Panel (A) shows the predicted log-intensity from the barrier SPDE model. Panel (B) shows the difference between both predictions, computed as barrier minus standard SPDE log-intensity.

582 barrier definition explicit and reproducible, allowing users to adapt the connectivity
 583 structure to the ecological question, species, or region under study. This is particularly
 584 relevant at the global scale, where decisions about narrow passages, islands, artificial
 585 channels, or semi-enclosed seas can strongly affect the implied spatial dependence.
 586 Therefore, MOBIE is not only a visualization tool, but a key part of the modelling
 587 workflow.

The simulated examples illustrate the flexibility of the framework under different response types commonly used in marine SDMs. The spatial Gamma example showed that the model can recover fixed effects and spatial dependence for positive abundance or biomass data. The spatio-temporal Gaussian example showed that the approach can represent continuous responses evolving over time while maintaining realistic marine connectivity. The Bernoulli example confirmed that the framework can also be applied to presence and absence data, although with greater uncertainty, as expected for binary observations.

The Atlantic cod case study demonstrated the usefulness of the framework for real survey data. Using a hurdle model, the occurrence and positive biomass components were modelled separately and then combined to obtain a hurdle-corrected prediction of relative biomass. The resulting spatial pattern identified high predicted biomass along northern Atlantic shelf systems, while reducing predictions in offshore areas or regions with low probability of occurrence (Fahay, 1999). This illustrates how global barrier models can produce ecologically interpretable predictions for species whose distributions are shaped by coastlines, shelf habitats, and regional marine connectivity.

Reef-building corals (order Scleractinia) are distributed throughout tropical and subtropical oceans, with their greatest diversity occurring in the Indo-Pacific region, particularly within the Coral Triangle, while lower-diversity assemblages occur in the Atlantic and eastern Pacific (Spalding, Ravilious, & Green, 2001; Veron & Stafford-Smith, 2000). The coral case study further showed how the barrier formulation can affect predictions in presence-only models. By comparing a global LGCP fitted with and without barriers, we showed that the inclusion of barrier structures changes the spatial propagation of predicted intensity, especially around complex coastal and island systems. This comparison was not intended as a standard model-selection procedure, but as a diagnostic of how different assumptions about ocean connectivity affect the predicted distribution. In this context, the barrier model provides a more physically realistic representation of spatial dependence than an unconstrained spherical SPDE model.

Several challenges remain. Barrier definitions should be ecologically justified and may vary across species, life stages, dispersal capacities, or oceanographic conditions. Future developments could consider implementing partially permeable or transparent barriers, where connectivity is reduced but not completely blocked, as well as dynamic barriers, where directionality can change, driven by ocean currents, temperature fronts, sea ice, or other time-varying environmental processes (Le-Bert Heyl, van Niekerk, & Rue, 2026). In addition, computational cost may increase when using high-resolution meshes, long time series, or multiple large ecological datasets. In this direction, recent approaches such as sequential consensus inference (Figueira, Conesa, López-Quílez, & Paradinas, 2025) provide a promising route for reducing computational burden while retaining much of the flexibility of integrated Bayesian models.

Overall, the proposed framework represents an important step towards a comprehensive spatio-temporal analysis of global species distribution models. By combining spherical geometry, spatial and spatio-temporal dependence, explicit representations of marine connectivity, and practical tools for barrier and mesh construction, the

methodology establishes a reproducible foundation for a new generation of global ecological models. Beyond the examples considered here, the framework opens the door to more sophisticated developments, including preferential sampling models, multivariate and coregionalized approaches, joint species distribution models, integrated analyses of multiple data sources, and large-scale spatio-temporal ecological assessments. Together with MOBIE and recent advances in scalable Bayesian inference, these developments provide a pathway towards increasingly realistic and operational global SDMs capable of addressing the complexity of marine ecosystems under global change.

Acknowledgements. DC thanks support by grants RED2024-153680-T and PID2022-136455NB-I00, both funded by Ministerio de Ciencia, Innovación y Universidades of Spain (MCIN/AEI/10.13039/501100011033/FEDER, UE) and the European Regional Development Fund. MC acknowledges support by grants PID2024-162762OB-I00 (Oceanic) and PID2020-118097RB-I00 (ProOceans) funded by Ministerio de Ciencia, Innovación y Universidades of Spain (MCIN/MCIN/AEI/10.13039/501100011033/FEDER, UE). This work was supported by the OSCARS-funded project FAME. The authors acknowledge the OSCARS project, which has received funding from the European Commission’s Horizon Europe Research and Innovation programme under grant agreement No. 101129751.

Data availability

The data and code used in this study are publicly available in the following repository: <https://github.com/AlbaFuster/Code-global-barrier>. This repository contains all the necessary materials to reproduce the analyses and results presented in our paper, including detailed instructions for use.

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