Estimating scale-dependent covariate responses using two-dimensional diffusion derived from the SPDE method

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Acknowledgements: We thank everyone involved in the collection, processing and collation of trawl survey and bird count data.

Author contributions: M. Lindmark conducted the simulation testing and the Breeding Bird case study. Sean C. Anderson contributed to software writing, and wrote simulation tests. J. T. Thorson derived statistical methods, wrote software, conducted the Bering Sea case study, and curated the Breeding Bird case study data. All authors discussed and interpreted results, and wrote the paper together.

Data Availability Statement: Code and data to reproduce the results are available on GitHub (`https://github.com/maxlindmark/covariate_diffusion`) and will be deposited on Zenodo upon publication.

Running head: Covariate-diffusion SPDE-based SDMs

Abstract

1. Species distribution models (SDMs) are widely used to standardize spatially unbalanced data, project climate impacts, and identify habitat for conservation. SDMs typically estimate the impact of local environmental conditions by applying a pointwise basis expansion, thereby estimating a dome-shaped or non-parametric "environmental response function". However, ecological responses integrate across local habitat conditions, such that the species density depends on habitat at the location of sampling but also at nearby locations.

2. To address this, we extend methods from the Stochastic Partial Differential Equation (SPDE) method that is widely used in INLA, which approximates spatial correlations based on local diffusion over a finite-element mesh (FEM). We specifically introduce the sparse inverse-diffusion operator on a FEM, and apply this operator to covariates to efficiently calculate a spatially weighted average of local habitat that is then passed through pointwise basis-expansion to predict species densities. We show that this operator has several useful properties, i.e., conservation of mass, linear computational time with spatial resolution, and a uniform stationary distribution, where the latter ensures that estimated responses are invariant to linear (scale and offset) transformations of covariates.

3. We test this covariate-diffusion method using a simulation experiment, and show that it can correctly recover a non-local environmental response while collapsing to a local (pointwise) response when warranted. We apply it to monitoring data for 25 bottom-associated fishes in the eastern Bering Sea and 20 bird species in the western United States. This application confirms that non-local responses in the eastern Bering Sea case study are parsimonious for 25 species-maturity combinations, while 20 collapse to the null method. Estimates suggest that some species-maturity combinations avoid proximity to the continental slope, beyond what is predicted by local bathymetry in isolation. By contrast, in only 2 of the 20 bird species is the diffused human population density covariate more parsimonious than the original covariate.

4. The covariate-diffusion method introduced here constitutes a fast and efficient approach to modelling non-local covariate effects. This flexible method may be useful in cases when covariates influence nearby population densities, for instance due to movement of the sampled species or its important biological or physical drivers.

Keywords: Species distribution models, geostatistical models, Gaussian Markov random fields, diffusion, TMB, breeding bird survey, northeastern Bering Sea, spatial scale

Introduction

Characterizing spatial patterns in the abundance of organisms in relation to environmental factors, and how that affects dynamics of ecological communities, is central to spatial ecology. At local scales, the abundance of species and demographic processes are shaped by both local habitat conditions, such as physical structure, competition and predation, and larger-scale processes (Menge and Olson 1990). The latter could refer to e.g., temperature and climate indices such as the NAO (Millon *et al.* 2014), and variables related to the dispersal pathways (Gómez-Pompa *et al.* 1972, Jonsson *et al.* 2016). Understanding how processes across spatial and temporal scales interact to shape species distribution and community structure is an important area of research in these times of rapid shifts in species distributions (Pinsky *et al.* 2013, Roberts *et al.* 2019, McCabe and Cobb 2021).

Species distribution models (SDMs) fitted to local occurrence, count, or biomass data are key tools in spatial ecology (Elith and Leathwick 2009). They can be used to quantify species' distribution, abundance and realized environmental niche and thereby be used to forecast range shifts (Liu *et al.* 2023, Pinsky *et al.* 2018). Over time, there has been a trend towards larger data sets over broader spatial and temporal scales (Rollinson *et al.* 2021). This has led to more power to detect effects and estimate functional relationships between covariates and responses, but also challenges related to non-stationarity. Non-stationarity here refers to the situation where the relationship between covariates and responses varies across space and/or time (Banerjee *et al.* 2014, Rollinson *et al.* 2021). In regression-based SDMs, which is the focus of this study, this form of non-stationarity can be accounted for by specifying effects of covariates that are allowed to evolve through time or vary in space (Hastie and Tibshirani 1993, Bartolino *et al.* 2011, Thorson *et al.* 2023, Anderson *et al.* 2024). Some examples include allowing the association of bottom-dwelling fishes with depth to change over time as they shift their distribution due to warming (English *et al.* 2022), and allowing regional ocean condition indices to cause a density response that varies spatially (Lehodey *et al.* 1997, Thorson 2019).

Another challenge related to spatial non-stationarity that has received less attention is the scale-dependence of covariates. Typically, local covariates are used in regression-based SDMs to infer the relationship between habitat covariates and the response variable. However, the true habitat an individual uses corresponds to the area it integrates via individual movement. Hence, for sessile species, local covariates may be warranted, but as species mobility increases, local-scale covariates would increasingly underestimate the habitat use in a typical scenario with a limited sample size. One could average covariates (and/or the response) prior to fitting the model to address that the relevant spatial scale that links covariates to the response is larger than the observation scale (e.g., Lindmark *et al.* 2023, McKeon *et al.* 2024), or evaluate multiple scales and find which best fits data (Bartolino *et al.* 2012). However, a limitation of this approach is that it is impossible to know the optimal scale of aggregation beforehand, and the scale resulting in the strongest effect does not necessarily mean it is the most relevant scale.

In this study, we introduce an approach that involves applying a diffusion operator to a covariate within the SPDE framework. This allows us to estimate the optimal spatial scale for computing a weighted average of a covariate, and can be thought of as a way to measure the effective "habitat area" that individuals are integrating via movement. Using simulation testing, we show how this covariate-diffusion model can correctly recover diffused covariate effects, or collapse to the raw covariate, when no covariate diffusion is present. We then apply the covariate-diffusion model to two real-world datasets on bottom-associated fishes and birds, and find that it is a parsimonious model for more than half the species-maturity combinations in the fish case study, and approximately two of the 20 bird species.

Methods

Covariate-diffusion

The Stochastic Partial Differential Equation (SPDE) method (Lindgren *et al.* 2011) is widely used to define spatially correlated variables in statistical models. We briefly summarize the method here, before discussing how our covariate-diffusion model arises as a novel reuse of the underlying math.

At the highest level, the SPDE method seeks to specify a Gaussian random field (GRF) $\mathbf{Z}$, where the value of this random field z_s at a set of locations $s \in D$ within a spatial domain D follows a Matérn covariance function

$$\mathrm{Cov}(z(s_1), z(s_2)) = \tau^{-2} f(d(s_1, s_2), \kappa, \nu), \tag{1}$$

where $d(s_1, s_2)$ is the distance between two locations, $f(d(s_1, s_2), \kappa, \nu)$ is the Matérn correlation function, κ is the decorrelation rate, ν is the smoothness parameter, and τ^{-2} is the pointwise variance. This covariance function then allows the GRF to be evaluated at a fixed set of locations as a multivariate normal distribution

$$\mathbf{z} \sim \mathrm{MVN}(\mathbf{0}, \mathbf{V}), \tag{2}$$

where $\mathbf{V}$ is the matrix of covariance among those locations. We could then calculate the value of the GRF z^* at a new location using bilinear interpolation, represented by a matrix $\mathbf{A}$, $z^* = \mathbf{A}\mathbf{z}$.

In two-dimensional coordinates, and assuming that Matérn smoothness $\nu = 1$, the SPDE method then approximates this GRF as a Gaussian Markov random field (GMRF), i.e., by specifying a sparse inverse-covariance (a.k.a. "precision" matrix) $\mathbf{V}^{-1} = \mathbf{Q}$

$$\mathbf{z} \sim \mathrm{GMRF}(\mathbf{0}, \mathbf{Q}), \tag{3}$$

where evaluating the multivariate normal density function involves the precision matrix, and hence can be directly calculated from $\mathbf{Q}$ without matrix inversion. Importantly, the sparse precision matrix can also be constructed directly using the SPDE method

$$\mathbf{Q} = \tau^2(\kappa^4\mathbf{M_0} + 2\kappa^2\mathbf{M_1} + \mathbf{M_2}), \tag{4}$$

where $\mathbf{M}_0$ is a diagonal matrix, $\mathbf{M}_1$ has first-order adjacency within a triangulated mesh, and $\mathbf{M}_2$ has second-order adjacency. These three matrices are typically constructed by lower-level software (e.g., the R package `fmesher` Lindgren 2023), and fitting this model does not require advanced

understanding of the model derivation. However, we here summarize the underlying theory to introduce our extension.

In particular, the SPDE approximation to a GMRF is derived by specifying a diffusive process (the partial differential equation from the method's name) and a stochastic "shock" ϵ as a simultaneous equation involving our GMRF $\mathbf{z}$

$$\kappa^2 \tilde{\mathbf{C}} \mathbf{z} = -\mathbf{G}\mathbf{z} + \epsilon, \tag{5}$$

$$\epsilon \sim \mathrm{MVN}(\mathbf{0}, \tau^{-2} \tilde{\mathbf{C}}), \tag{6}$$

where $\tilde{\mathbf{C}}$ is a diagonal matrix and $\mathrm{diag}(\tilde{\mathbf{C}})$ is the volume of the linear basis functions centered at each location and $\mathbf{G}$ is a sparse matrix representing the spatial overlap between basis functions (i.e., is zero for nonadjacent locations). Subtracting the right-hand-side from the left yields

$$\left(\kappa^2 \tilde{\mathbf{C}} + \mathbf{G}\right) \mathbf{z} = \epsilon, \tag{7}$$

and then dividing the left-hand-side across and expressing as a GMRF yields

$$\epsilon \sim \mathrm{GMRF}(\mathbf{0}, \mathbf{Q}), \tag{8}$$

$$\mathbf{Q} = \left(\kappa^2 \tilde{\mathbf{C}} + \mathbf{G}\right) \tau^2 \tilde{\mathbf{C}}^{-1} \left(\kappa^2 \tilde{\mathbf{C}} + \mathbf{G}\right). \tag{9}$$

Multiplying out the quadratic form for the precision matrix then results in the original expression (Eq. 4), where $\mathbf{M_0} = \tilde{\mathbf{C}}$, $\mathbf{M_1} = \mathbf{G}$, and $\mathbf{M_2} = \mathbf{G}\tilde{\mathbf{C}}^{-1}\mathbf{G}$.

Having re-iterated the diffusion process that underlies the SPDE precision matrix, we now define a diffusion matrix $\mathbf{D}$

$$\mathbf{D}^{-1} = \left(1 + \kappa^2\right)^{-1} \tilde{\mathbf{C}}^{-1} \left(\tilde{\mathbf{C}} + \kappa^2 \tilde{\mathbf{C}} + \mathbf{G}\right), \tag{10}$$

where the inverse-diffusion $\mathbf{D}^{-1}$ has the same sparsity as $\mathbf{G}$, which follows first-order adjacency. This operator satisfies three desiderata:

1. *Conservation of mass*: Given a field approximated as vector $\mathbf{z}$ at the vertices of the finite-element mesh, N evenly spaced locations $\mathbf{s}$ that cover the domain, and bilinear interpolation matrix $\mathbf{A}$ that projects to those N locations, we can approximate the average value of the field by predicting and then averaging across those locations $\bar{x} = N^{-1}\mathbf{1}^T\mathbf{A}\mathbf{x}$. Pre-multiplying by the diffusion operator has (almost) no effect on this average mass, $\mathbf{1}^T\mathbf{A}\mathbf{x} = \mathbf{1}^T\mathbf{A}\mathbf{D}\mathbf{x}$, i.e., where the diffusion operator conserves the total value of $\mathbf{z}$;

2. *Invariance to centering or scaling*: Given that we approximate diffusion using a linear operator, we can apply a linear transformation to any vector $\mathbf{z}^* = a + b\mathbf{z}$, and this will result in the same linear transformation of the diffused version $\mathbf{D}\mathbf{z}^* = a + b\mathbf{D}\mathbf{z}$. For example, if we measure temperature in Celcius at a set of sites, convert to Farhenheit, and then apply the diffusion operator, this will be equivalent to applying the diffusion operator and then converting to Farenheit;

3. *Efficient computation*: The diffusion matrix $\mathbf{D}$ is "dense" (i.e., values become small but remain nonzero even as distances become large), and hence the time to compute $\mathbf{D}\mathbf{v}$ scales as S^2 where S is the number of sites (Fig. S1). However, we can instead calculate $\mathbf{D}\mathbf{v}$ efficiently by first calculating a sparse LU decomposition of $\mathbf{D}^{-1}$ and then applying this to $\mathbf{v}$. Doing so works directly with the sparse matrix $\mathbf{D}^{-1}$, and avoids computing or storing the dense matrix $\mathbf{D}$.

In the following, we therefore define a vector of covariate values $\mathbf{x}$ at the vertices of the finite-element mesh, where the covariate x^* is interpolated at a new location using the same interpolation matrix $x^* = \mathbf{A}\mathbf{x}$. We then replace the covariate value x^* for sample i at location s_i with its diffused value $\mathbf{A}\mathbf{D}\mathbf{x}$, and use $\mathbf{A}\mathbf{D}\mathbf{x}$ to predict local densities in a species distribution model. The effect of applying the diffusion operator and its effect on the total mass of the covariate is visualized in Fig. 1. We then estimate parameter κ (used to construct diffusion matrix $\mathbf{D}$) simultaneously with other regression coefficients representing habitat associations. As $\kappa \longrightarrow \infty$ in Eq. 10 then diffusion $\mathbf{D}^{-1} \longrightarrow \mathbf{I}$ and the diffused covariate collapses on its local value $\mathbf{D}\mathbf{x} = \mathbf{x}$. Alternatively, as $\kappa \longrightarrow 0$ then $\mathbf{D}\mathbf{x} = c\mathbf{1}$ and the diffused covariate collapses on an constant value c. We are therefore interested in

intermediate values of κ where $\mathbf{Dx}$ represents the impact of covariates within the neighborhood of a given location.

Testing the ability to recover diffusion with a simulation experiment

We used simulation testing to evaluate 1) how well the estimate for a diffused covariate could be recovered under varying observation error, 2) how often marginal AIC favoured the correct estimation model (diffusion or null model) in a self-and-cross experiment, 3) how well the diffusion parameters could be recovered under varying strengths of diffusion, and 4) how well the diffusion model can collapse to the null model (i.e, how well the diffusion model can match the null model estimates when data are simulated without diffusion). We simulated 200 datasets from a Poisson model with an observation-level random intercept in link space to allow for additional dispersion beyond the 1:1 mean-variance of the Poisson — a lognormal Poisson. Parameters were largely taken from a model fitted to counts of juvenile Pacific cod (*Gadus macrocephalus*) in a subsequent case study, with a scaled depth covariate (subtracting the mean and dividing by the standard deviation). Each data set contained 15592 spatially correlated observations, and for every dataset, a new GMRF was simulated. For a more detailed description of the models we refer to the northeastern Bearing Sea case study, see *Case studies*.

In the first exercise (questions 1 and 2), we generated data by simulating from models without and with covariate-diffusion. In the former, we set the intercept β_0 to -0.4, the linear effect of the raw or diffused covariate β_j to -2.4, the scalar of the precision matrix $\log(\tau)$ to -1.4, and the decorrelation rate $\log(\kappa)$ to -0.8. For the diffusion model, we in addition set the strength of the diffusion $\log(\kappa)$ to 2.5 (which corresponds to moderate diffusion). In both operating models, we varied the observation level standard deviation, setting σ_η to 0.1, 1, and 2, and tested how well both models could return the true depth coefficient, and how often marginal AIC favoured the correct operating model.

In the second exercise (questions 3 and 4), we simulated data from a diffusion model to evaluate how well the true value of the diffused covariate could be retrieved, given varying strengths of the diffusion, and how often marginal AIC favoured the correct operating model. We used the same

parameters for the diffusion model as above ($\sigma_\eta = 1$), and set $\log(\kappa)$ to 0 (strong diffusion), 2.5 (moderate diffusion), and 5 (low diffusion).

Case studies

To illustrate a diffused covariate in practice, we also present two real-world case studies. In the first case study, we use count data for 20 species from the US Breeding Bird Survey (Sauer *et al.* 1997) in the western United States (westward of Wyoming, Colorado, Montana, and New Mexico) in 2019. We test if there is support for non-local effects of log human population density. This could, for instance, indicate a response to urbanization affecting the habitat quality. For example, outside densely populated areas there may still be large impacts of habitat due to infrastructure. We use marginal AIC to determine if the more complex covariate-diffusion model is supported. The second case study is based on bottom trawl survey data from the northeastern Bering Sea in 2019, collected by the NOAA Alaska Fisheries Science Center (AFSC) using a fixed station design. Each trawled site contains information on catch in numbers of 45 species-maturity combinations. Here we test if there is support for non-local effects of sea floor depth. A diffused depth effect could for instance indicate a response to being near (but not actually on) the continental slope.

In both case studies, we modelled the counts at each site using a lognormal Poisson observation model and a log link

$$Y_{s,t} = \log(\mu_{s,t}), \tag{11}$$

$$\mu_{s,t} = \boldsymbol{X}_{s,t}\boldsymbol{\beta} + \alpha_g + \omega_s, \tag{12}$$

$$\omega_s \sim \mathrm{MVN}(\mathbf{0}, \Sigma_\omega), \tag{13}$$

where $\mu_{s,t}$ represents the mean count, $\boldsymbol{X}_{s,t}$ is the design matrix, α_g is an observation-level random intercept, and ω_s represents spatial random effects drawn from a Gaussian Markov random field with inverse precision (i.e., covariance) matrix Σ_ω constrained by a Matérn covariance function. We constructed meshes using the function `fm_mesh_2d()` in the R package `fmesher` (Lindgren 2023), using a cutoff distance (minimum triangle edge length) of 0.1 degrees in the northeastern

Bering Sea case study (1295 knots) and 1 degree in the Breeding Bird Survey (170 knots) (Figs. S3–S2).

Estimation process

We fit the SPDE-based spatial models in the simulation experiment and the case studies using the R (R Core Team 2024) package `TMB` (Kristensen *et al.* 2016), with matrices in Eq. 5 constructed with the R package `fmesher` (Lindgren 2023). Parameter estimation is done via maximum marginal likelihood using the non-linear minimizer `nlminb` (R Core Team 2024).

Results

The covariate-diffusion estimation model is able to retrieve the true parameters accurately both when the underlying model ("operating model") generating the data had covariate-diffusion and when it did not, since the diffusion model reverts to the sub model without covariate-diffusion as κ becomes large (Fig. 2). However when the operating model is a covariate-diffusion model, the null estimation model leads to biased parameter estimates (Fig. 2a). We also find that marginal AIC favours the covariate-diffusion model in >98% of cases when the operating model is covariate-diffusion (Fig. 2a), and favours the null model in >94% when the operating model is null (Fig. 2b). Neither the ability to retrieve the true parameter estimate nor the assignment based on marginal AIC are affected by the observation error standard deviation given the ranges tested here (Fig. 2). We also find that marginal AIC identifies the true operating model more frequently when the strength of the diffusion is larger—86–98% of cases (Fig. 3a–b)—but for low diffusion, marginal AIC favours the the null model (Fig. 3c). The covariate-diffusion model is able to retrieve the true parameter value on average regardless of the strength of the diffusion, but the spread of individual estimates is larger when the diffusion is stronger (Fig. 3a).

Our case studies show that covariate diffusion is supported to varying degrees in both bird species and fish groups. In two of 20 bird species, covariate-diffusion is supported for the human population density covariate as they have $\Delta\text{AIC} > 2$ (Fig. 4a). In contrast, we find support for

covariate diffusion of a quadratic depth effect in 26 out of 45 species-maturity combinations in the eastern Bering Sea case study on fishes (Fig. 4b). In both case studies, a $\Delta\text{AIC} = -2$ indicates that the covariate-diffusion and the null model have the same marginal log likelihood, and the correlation between the raw and diffused covariate approaches 1 (Fig. 4).

A lower correlation between the diffused and raw covariate is typically found in species where the covariate-diffusion model is supported (Fig. 4). For example, in the Breeding Bird case, the covariate-diffusion model is not supported for the common starling (*Sturnus vulgaris*; top row) and the diffused covariate (middle column) is nearly identical to the original covariate (left column), while for black-headed grosbeak (*Pheucticus melanocephalus*; bottom row) the human population density covariate is smoothed with a relatively strong diffusion ($\log \kappa = -8.07$) (Fig. 5b). Similarly for the example fishes from the northeastern Bearing Sea case, in adult Alaska pollock (*Gadus chalcogrammus*), the depth covariate from the covariate-diffusion model is nearly identical to the raw covariate, while for capelin (*Mallotus villosus*), the diffusion is strong ($\log \kappa = -7.44$), and the covariate exhibits a smoother pattern.

For several species-maturity combinations in the fish case study, there is a notable difference in the partial effect of depth on density (Fig. S4). However, the covariate-diffusion model and the null model often generate similar predictions, even in cases of strong diffusion, presumably because the spatial random effects can change between the models (Figs. S5, S6).

Discussion

We have introduced a sparse inverse-diffusion operator based on the SPDE method, which can be used to efficiently model non-local covariate effects such as to approximate the effective habitat area that individuals integrate via movement. Specifically, when applied to a covariate, this operator calculates a spatially weighted average covariate given the estimated range of the diffusion processes. With simulation testing, we have demonstrated that the diffusion model can correctly identify the underlying processes model and estimate the density response to the diffused covariate.

We then tested the approach on spatial models fitted to datasets for bird and fishes. Covariate-diffusion was more parsimonious than the null model for only two of 20 bird species, but for a majority of species-maturity combinations in fishes. As an example of interpretation, for some species-maturity combinations in the fish case study, the partial effect of depth was smaller for the covariate diffusion model than the null model near the continental shelf slope suggesting that these groups avoid these habitats despite being of similar depths to other more inshore areas. Hence, our approach could aid generating hypothesis as to what drives non-stationary in across space, which is important for improving large-scale species distribution modeling (Rollinson *et al.* 2021).

Covariate-diffusion could result from any ecological teleconnections such that local ecological properties are influenced by patterns happening at a broader scale. For example, fish move over time and therefore their body condition (how plump they are given their length) may be affected by the combination of habitat and spatially varying prey they encounter over their lifetime (Lindmark *et al.* 2023). Covariate diffusion could represent how this broader scale of conditions the fish moved through might affect their body condition. Alternatively, a species may be stationary with environmental process changing around them. For example, the number of eggs produced by sessile clams may be influenced by environmental conditions as ocean currents move water past the clams. Covariate diffusion could represent how this broader scale of experienced environment might affect clam fecundity.

We observe that predictions from the diffusion model and the null model tend to be similar. While both the covariate and the estimate of its coefficient change when the diffusion model is applied and supported, the predicted counts do not substantially differ between the two models, partly because the spatial random effects also change. Which model to use then depends on the objectives of the analysis—whether it is to learn about ecologically relevant scales of covariates and non-local effects or if a model that generates similar predictions by placing additional variation in the spatial random effects will suffice. Since we have also shown that the diffusion model can revert to a non-diffused model in the absence of diffusion, the diffusion model can be applied even though it is not known whether diffusion is supported a priori at little cost.

We recommend two topics for future research. The first is to augment our covariate-diffusion model by incorporating advection, i.e., where local densities respond to environmental conditions that are centered on a location that is geographically distant. This "covariate-advection" is feasible using the SPDE method (Clarotto *et al.* 2023) and would presumably represent advective movement, e.g., where densities during summer sampling respond to habitat conditions in a winter habitat. Second, we note that covariate-diffusion collapses to an index of regionally averaged conditions as diffusion becomes large. In this case, fitting a spatially varying coefficient (SVC) (Hastie and Tibshirani 1993, Gelfand *et al.* 2003) response to the diffused covariate across multiple years would allow a wide range of model behaviors, from a stationary and local response to a non-stationary response to a regional climate index.

We note several drawbacks to the covariate-diffusion approach. First, the approach replaces the high-resolution covariate measured at each unique location with an interpolated value that is defined at each vertex of the finite-element mesh. This mesh can be defined at a high resolution, but still requires some loss of fine-scale variation. Second, although computationally efficient due to working with the sparse inverse diffusion matrix, the approach is still more computationally intensive than fitting a model without covariate diffusion. Third, the model requires users to define covariate values not just for the location of samples, but at all locations across a given domain. This results in a more-complex user interface than the regression models typically used for SDMs and will therefore require some consideration before integrating into GMRF- and TMB-based SDM software such as sdmTMB (Anderson *et al.* 2024) or tinyVAST (Thorson *et al.* 2024).

Despite these drawbacks, we conclude that covariate-diffusion using the SPDE method is computationally efficient, statistically performant, and ecologically important for a wide range of species. We therefore recommend that ecologists estimate non-local habitat responses across the wide range of studies applying SDMs.

Funding

M.L. was supported by a research grant from the Swedish Research Council Formas (grant no. 2022-01511 to Max Lindmark).

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Figures

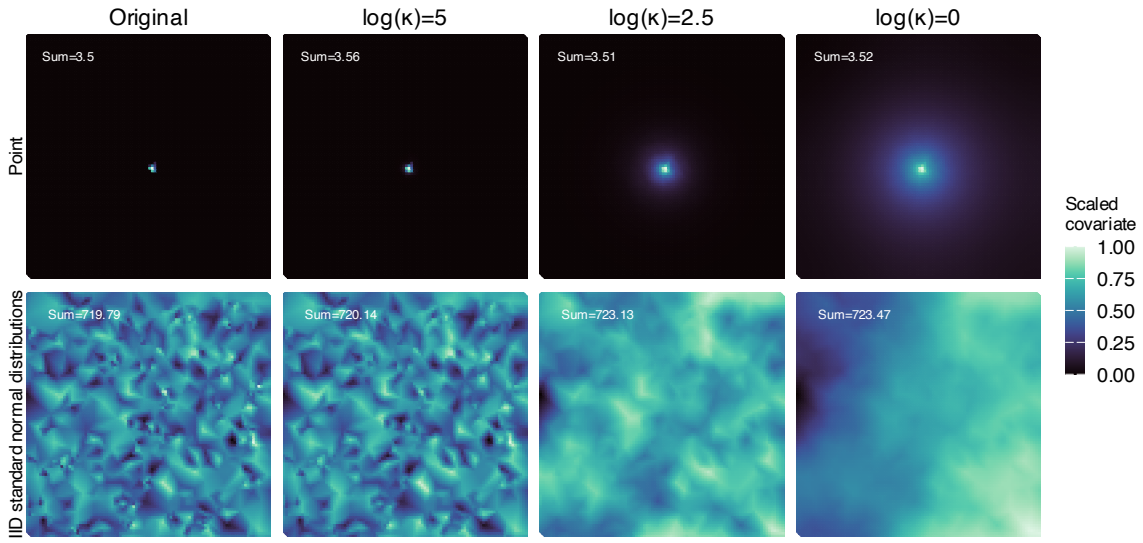

Figure 1: Applying the diffusion operator $\mathbf{D}$ when interpolating covariate $\mathbf{x}$ with interpolation matrix $\mathbf{A}$ to vertices of the finite-element mesh largely conserves the mass across different values of κ (i.e., $\sum \mathbf{Ax} \approx \sum \mathbf{ADx}$). In the top row, the diffusion is visualised for a single central point and in the bottom row diffusion is applied to a vector of draws from IID standard normal distributions to visualise diffusion on the full covariate field. Columns correspond to different κ values, from large κ (low diffusion) to small κ (high diffusion). Note that the covariate values are scaled within each kappa scenario to visualise the diffusion; the number in the top left corresponds to the total mass of the covariate.

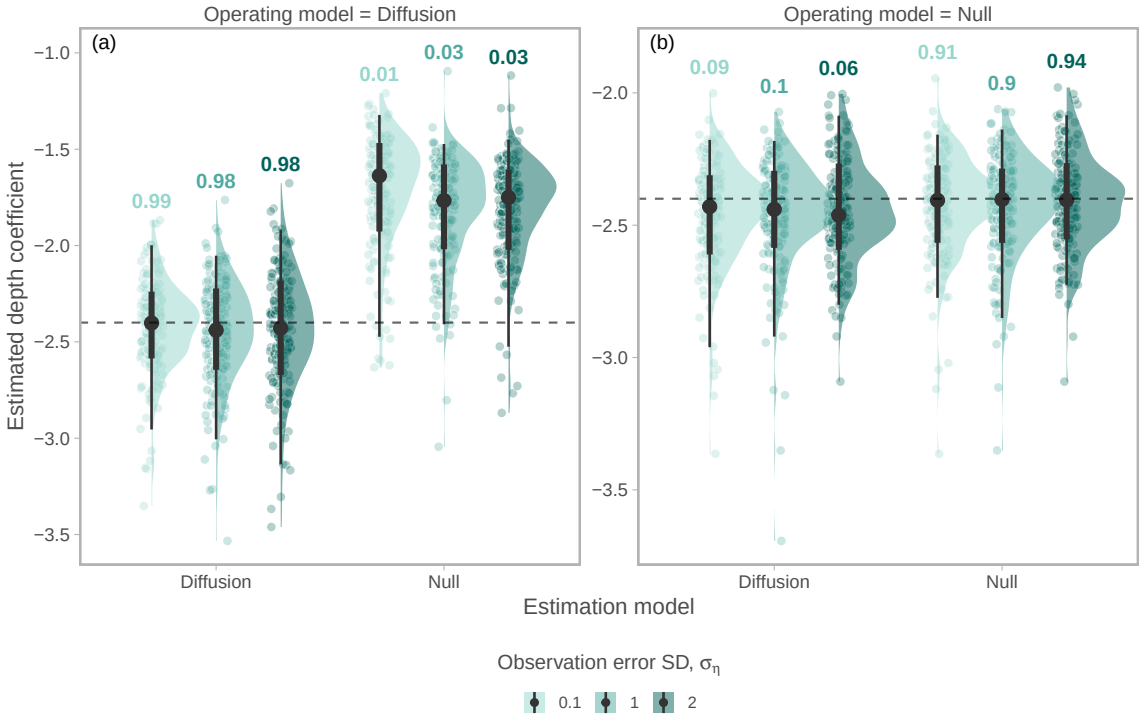

Figure 2: The diffusion model can recover diffused covariate effects and collapse to the null model in the absence of diffusion. Simulation testing the ability to recover the true estimated depth coefficient for diffusion and null operating models (left and right, respectively), for diffusion and null models (x-axis), for three levels of lognormal Poisson observation error σ_η (color). Each point represents a fit from a simulated data set, black points and vertical lines correspond to the median, 50%, and 95% quantile range. Horizontal lines correspond to the true value. Numbers above vertical bars correspond to the proportion of simulated datasets (n=200) assigned to the estimation model (per value of σ_η) based on marginal AIC.

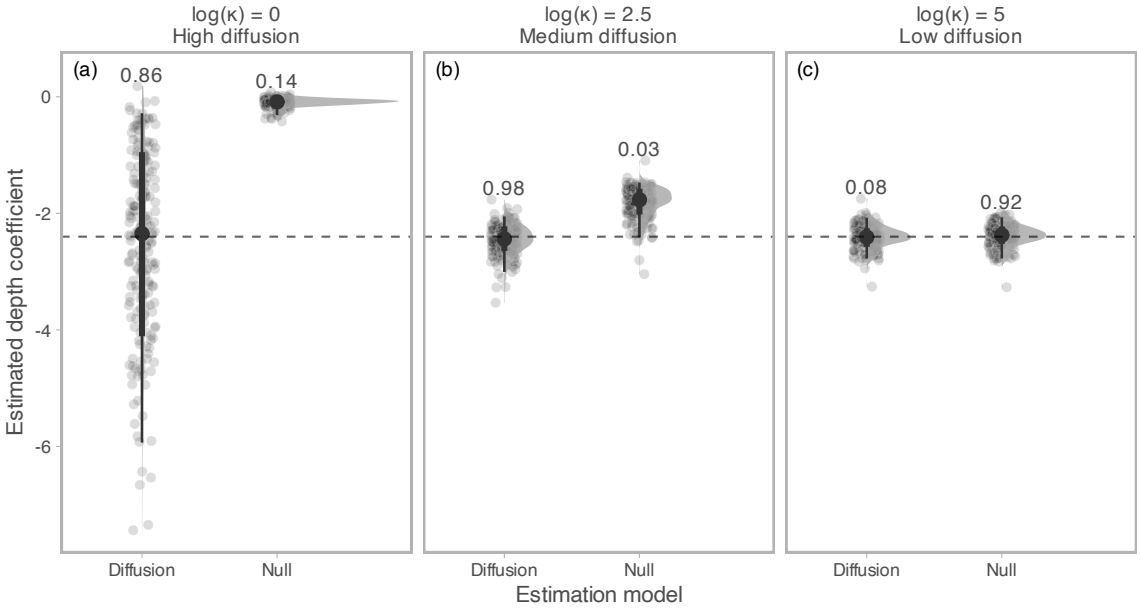

Figure 3: As the diffusion declines (κ increases, from left to right column), the difference between estimated depth coefficients from the diffusion and null models decreases (from left to right). Each point represents a fit from a simulated data set, black points and vertical lines correspond to the median, 50%, and 95% quantile range. Horizontal lines correspond to the true value. Numbers above vertical bars correspond to the proportion of simulated datasets (n=200) assigned to estimation model based on AIC.

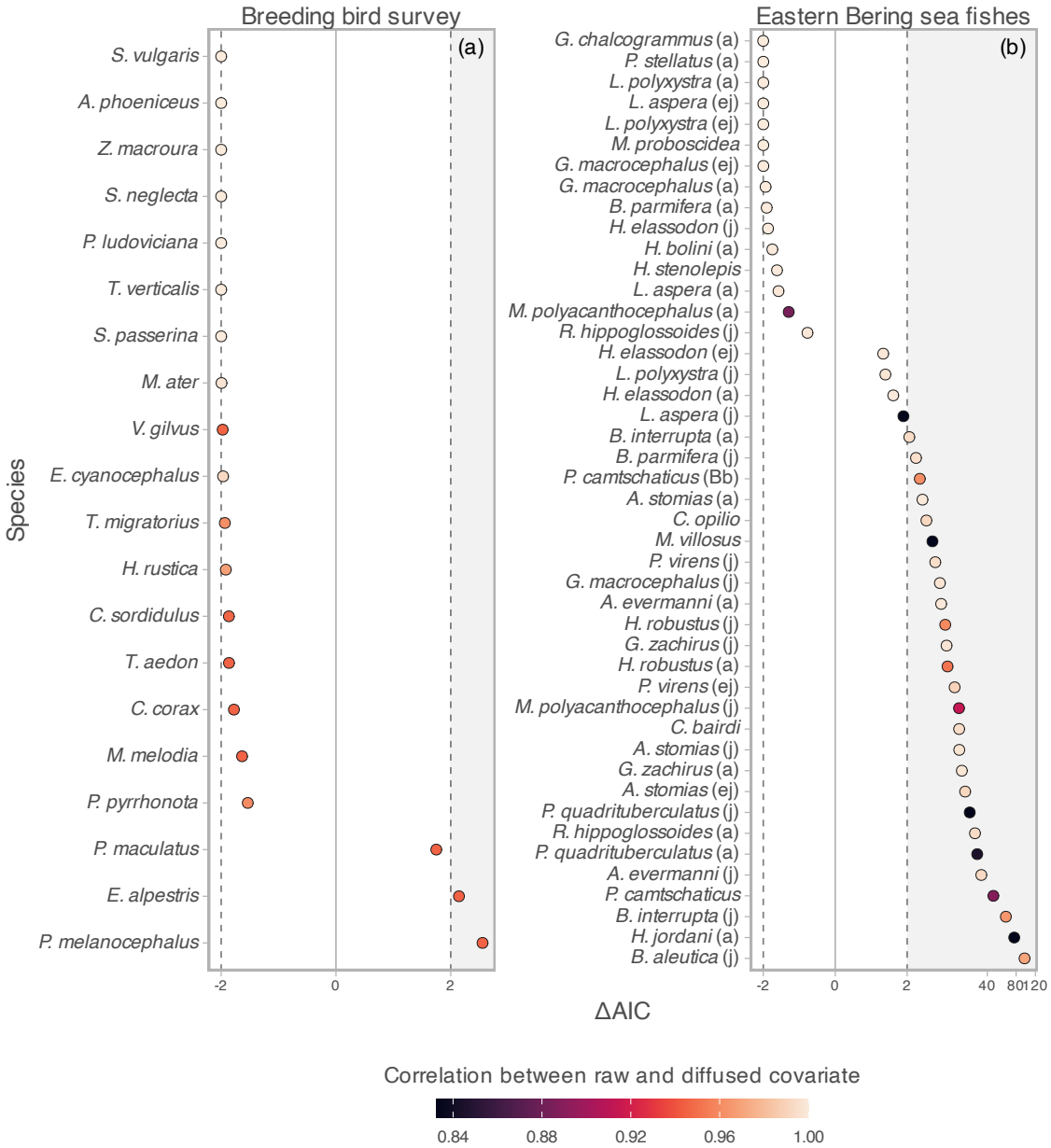

Figure 4: Marginal AIC favours covariate-diffusion in more than half of fishes and two bird species. The points depict delta marginal AIC between the null and diffusion model, where positive values indicate support for the diffusion model and negative values indicate support for the null model. Point colours correspond to the correlation between the raw and the diffused covariate. Points in the grey rectangle have delta AIC>2, indicating strong support for the diffusion model. Points within the two vertical dashed lines have inconclusive ΔAIC results. Letters in brackets in the Eastern Bering sea fish case study refers to the life stage (j=juvenile, a=adult, ej = early juvenile), except for *P. camtschaticus*, where Bb stands for Bristol bay. Note the x-axis is fourth-root power transformed.

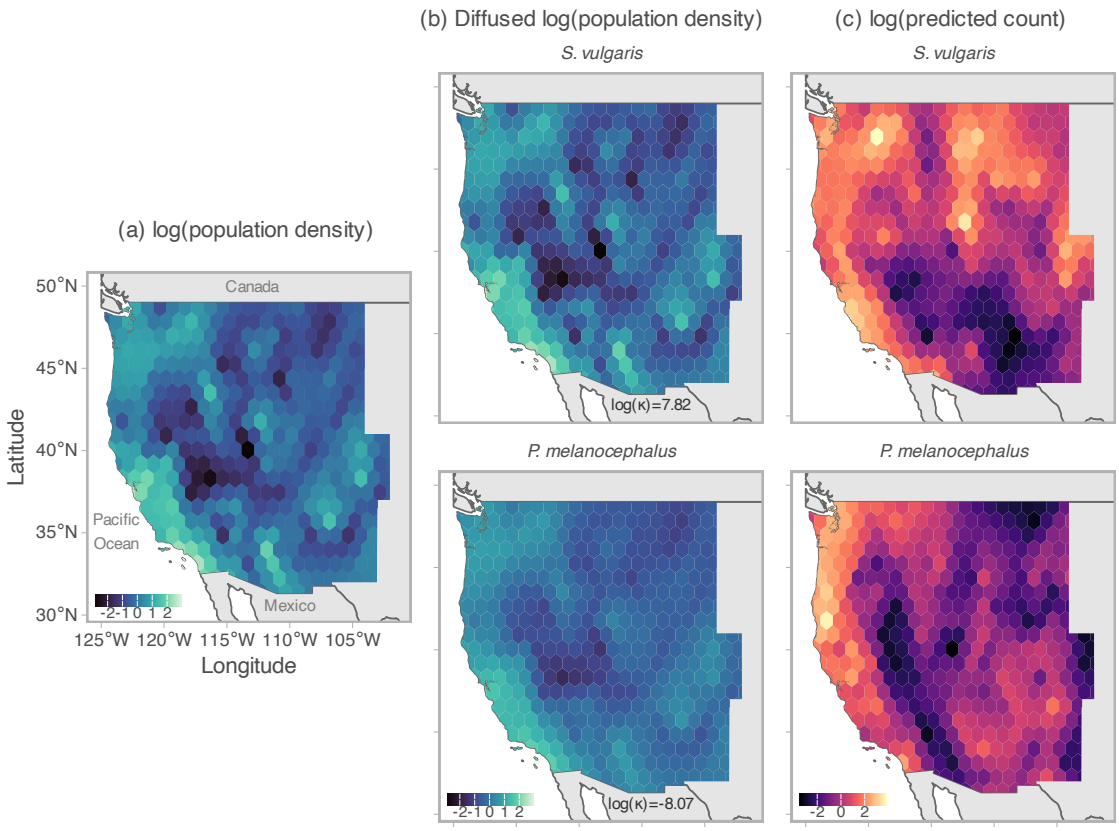

Figure 5: Human population density covariate, a diffused version of the covariate, and predicted counts from the breeding bird case study. Panel (a) depicts the raw human population density covariate. Panel (b) depicts the diffused covariate for two species with contrasting support for diffusion. Common starling (*Sturnus vulgaris*) in the top row does not show support for the diffused covariate and the diffusion is estimated to be small whereas black-headed grosbeak (*Pheucticus melanocephalus*) in the bottom row shows strong support for the diffused covariate and has a relatively strong estimated diffusion. The strength of the diffusion ($\log(\kappa)$) is shown towards the bottom of the (b) panels, where a low value indicates strong diffusion. Panel (c) depicts the predicted log counts for the two species.

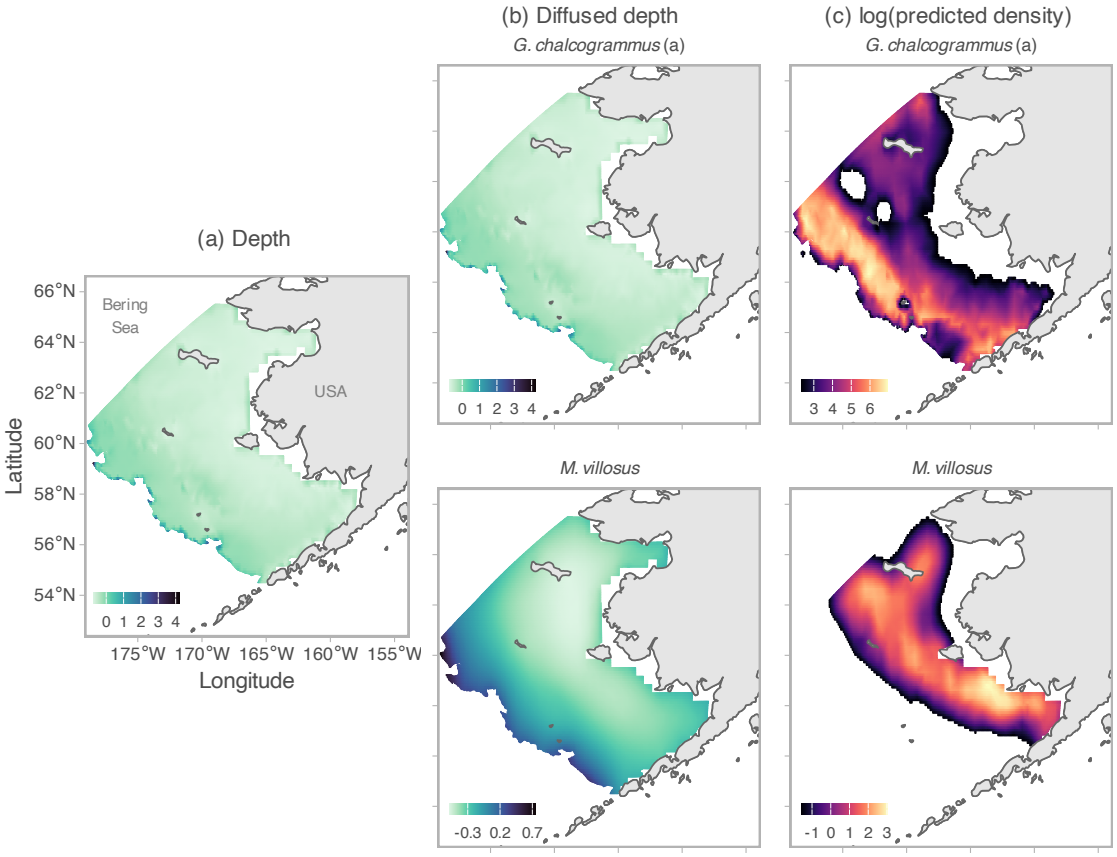

Figure 6: Bottom depth covariate, a diffused version of the covariate, and predicted counts from the northeastern Bering sea bottom trawl data. Panel (b) depicts the diffused covariate for two species with contrasting support for diffusion. Adult Alaska pollock (*Gadus chalcogrammus*) in the top row does not support the diffusion model and the diffused covariate is similar to the raw covariate, while capelin (*Mallotus villosus*) in the bottom row shows strong support for the diffusion model. The strength of the diffusion ($\log(\kappa)$) is shown in the bottom-right corner of the (b) panels; a low value indicates strong diffusion. Panel (c) depicts the predicted log counts for the two species (values $< 1\%$ of the maximum density are omitted for visualization).