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Research article

Spatially varying coefficients can improve parsimony and descriptive power for species distribution models

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Species distribution models (SDMs) are widely used to relate species occurrence and density to local environmental conditions, and often include a spatially correlated variable to account for spatial patterns in residuals. Ecologists have extended SDMs to include spatially varying coefficients (SVCs), where the response to a given covariate varies smoothly over space and time. However, SVCs see relatively little use perhaps because they remain less known relative to other SDM techniques. We therefore review ecological contexts where SVCs can improve the interpretability and descriptive power from SDMs, including local responses to regional indices that represent ecological teleconnections; density-dependent habitat selection; spatially varying detectability; and context-dependent covariate responses that represent interactions with unmeasured covariates. We then illustrate three additional examples in detail using the vector autoregressive spatio-temporal (VAST) model. First, a spatially varying decadal trends model identifies decadal trends for arrowtooth flounder *Atheresthes stomias* density in the Bering Sea from 1982 to 2019. Second, a trait-based joint SDM highlights the role of body size and temperature in spatial community assembly in the Gulf of Alaska. Third, an age-structured SDM for walleye pollock *Gadus chalcogrammus* in the Bering Sea contrasts cohorts with broad spatial distributions (1996 and 2009) and those that are more spatially constrained (2002 and 2015). We conclude that SVCs extend SDMs to address a wide variety of ecological contexts and can be used to better understand a range of ecological processes, e.g. density dependence, community assembly and population dynamics.

Keywords: hierarchical model, joint species distribution model, nonstationarity, random slope, SDM, spatially varying coefficient



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Introduction

Many taxa show rapid shifts in spatial distribution due to ongoing climate change and economic development, which is reshaping community composition and ecosystem function worldwide (Roberts et al. 2019, Huntington et al. 2020, McCabe and Cobb 2021). Meanwhile, dispersal processes cause local distribution, abundance, and diversity to be impacted by both local and regional ecological conditions (Menge and Olson 1990). Meta-communities are similarly impacted across spatial scales by local conditions, regional species pools, and the spatial configuration of habitats (Leibold et al. 2004). Spatial ecology seeks to characterize resulting spatial patterns and identify the environmental conditions and community dynamics that drive them.

Species distribution models (SDMs) are an important and widespread technique used by spatial ecologists to relate species occurrence or abundance to localized environmental or habitat characteristics (Elith and Leathwick 2009). SDMs are increasingly used to inform conservation efforts and measure shifts in habitat utilization over time (Srivastava et al. 2019, Titley et al. 2021). Factors like biotic interactions between species can drive community composition and ecosystem dynamics in ways that are spatially autocorrelated (via dispersal patterns, Earn et al. 2000) and difficult to predict from environmental variables alone (Cazelles et al. 2016). Different morphological, behavioral and life-history characteristics can also mediate how species interact with their environment and with each other (Cadotte et al. 2011, Brown et al. 2014); thus, identifying relationships between species traits and the environment has remained a central goal of community ecology for decades (Legendre et al. 1997, McCune et al. 2002). For example, tooth morphology dictates predator–prey interactions, foraging time (e.g. diurnal, nocturnal) influences whether or not species compete for resources, and species longevity is correlated with maximum depth for Pacific rockfishes *Sebastes* spp. (Mangel et al. 2007). The failure to account for spatial autocorrelation and other (stochastic and biological) factors that influence species occurrence is evident in the limited predictive capacity and inflated type I error of single-species SDMs (Cruse et al. 2014).

Joint SDMs (JSDMs) extend univariate SDMs by predicting distribution and density for multiple categories (e.g. ages, life stages, species) simultaneously. Joint SDMs offer the potential to estimate how species traits result in similar or different responses to local environmental conditions (Ovaskainen et al. 2017). Multispecies JSDMs explicitly account for shifts in species co-occurrence across environmental gradients and, as such, have the potential to explain a greater amount of the variance in species distributions than models that rely solely on abiotic predictors (Norberg et al. 2019). In particular, sharing information across ages, life stages, or species is likely to improve predictive performance for species that have limited information (Hui et al. 2013, Thorson et al. 2016). Although the greater complexity of multivariate models can dramatically improve ecological inferences, these SDMs are commonly implemented with

the assumption that species respond to local environmental conditions, despite some evidence that inclusion of regional effects can improve model performance (O’Leary et al. 2022).

The increased use of both univariate and multivariate or joint SDMs is aided by improved access to long-term and spatially expansive data sets, though these also provide new analytical challenges. In particular, models that are fitted to large spatial areas often assume that a covariate has the same effect in all locations (a ‘stationary effect’), and data over large geographic areas allow increased power to detect changes in covariate responses across space (‘spatial nonstationarity,’ Rollinson et al. 2021). Spatial nonstationarity has previously been addressed using geographically weighted regression (Brunsdon et al. 1996) or spatio–temporal exploratory models (Fink et al. 2010), where both approaches involve fitting a series of models and then combining results post hoc. However, these approaches require, respectively, tuning a kernel weighting parameter (i.e. using cross-validation) or a priori spatial stratification when fitting models. As an alternative to these ‘two-stage approaches,’ spatially varying coefficient (SVC) models were developed as a flexible extension of regression models to deal with complex correlation structures, nonstationarity, and scale-dependencies (Hastie and Tibshirani 1993, Gelfand et al. 2003). Specifically, SVC models allow a specified coefficient to vary across space, i.e. the response curve for covariate x changes smoothly across the modeled domain. By doing so, SVC models can improve model fit and strengthen inferences about mechanistic relationships by apportioning residual variance to spatial processes (Finley 2011, Rollinson et al. 2021). SVC capabilities have been coded into many of the R packages (www.r-project.org) that support SDMs (mgcv: Wood et al. 2016, VAST: Thorson and Barnett 2017, inlabru: Bachl et al. 2019, spBayes: Finley and Banerjee 2020, sdmTMB: Anderson et al. 2022). Despite this, a citation analysis for SVC papers confirms that they are a small (<10%) fraction of studies using species distribution models (Fig. 1), although see Rollinson et al. (2021) for recent examples of their ecological use.

We assert that SVCs can improve the performance and interpretation of conventional and joint SDMs, and suspect that their underuse arises from a lack of familiarity with how or when to include them. We therefore proceed to identify seven ecological contexts when SVCs may result in a more detailed description of ecological processes. We then describe in detail three of these cases using a common statistical package VAST to demonstrate how disparate applications arise from a shared model structure.

Methods

Overview of spatially varying coefficients

Species distribution models (SDMs) are often fitted using some variant of a generalized linear model (GLM), so we first describe how spatially varying coefficients (SVCs) are implemented in this context. As a minimal example, GLMs

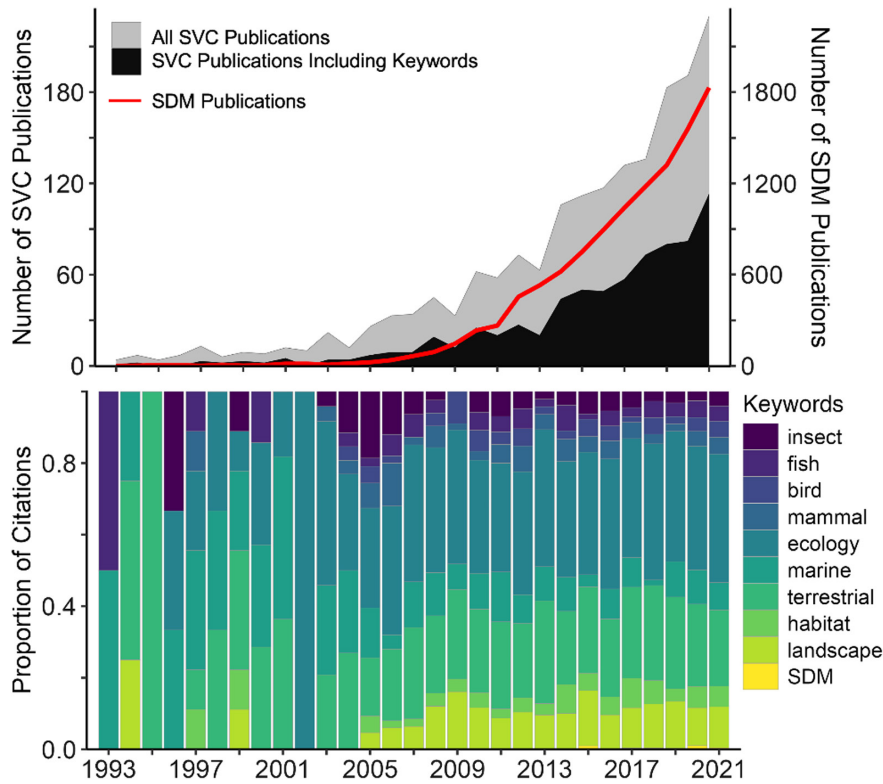


Figure 1. Numbers of publications that have referenced spatially varying coefficients (SVCs; gray area) since [Hastie and Tibshirani \(1993\)](#). The number of publications that referenced species distribution models (SDMs; red line) and the number of SVC publications that included one or more keywords indicating an ecological study (i.e. insect, fish, bird, mammal, ecology, marine, terrestrial, habitat, landscape and SDM) are also shown in the top panel (black area). Proportions of SVC publications that contain each keyword are illustrated in the bottom panel. Those that contained more than one keyword were used to calculate proportions for each applicable category (e.g. an SVC publication that contained the words ‘fish’ and ‘SDM’ was included in each of the two categories). Data Source: Google Scholar. Search terms for SVC publications included ‘spatially varying coefficient’, ‘spatially-varying coefficient’, or ‘spatially varying process’.

predict species density y_i for observation i as a function of covariate x_i :

$$\log(y_i) = \alpha + \beta x_i$$

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$$Y_i \sim g(y_i)$$

where α is the estimated intercept and β is the estimated log-linear response of species density y to covariate x . Here we specify a log-link function to ensure that species density y is non-negative and specify a probability distribution g for sampling data Y given predicted density y .

SDMs will often show spatial patterns in residuals $Y - y$, and are often extended to address spatial autocorrelation by specifying that the intercept varies smoothly as a function of location s :

$$\log(y_i) = \alpha_s + \beta x_i$$

Alternatively, an SVC model incorporates spatial variation in the response to covariates, where the slope β_s varies smoothly across locations s :

In practice, we envision that analysts will consider spatial variation in both the intercept and slope(s). In many cases, a smooth function is specified for the spatially varying intercept α_s and/or slope β_s ; in the following we will specify a Gaussian random field such that α_s and/or β_s follow a multivariate normal distribution with correlation based on the spatial distance among locations.

SVCs can be implemented using a wide variety of statistical models and estimation techniques. These models can be fitted in common statistical software, e.g. the R package (www.r-project.org) `mgcv` for generalized additive models ([Wood 2006](#)), using the formula notation:

$$\text{formula} = y \sim s(\text{lat}, \text{lon}) + s(\text{lat}, \text{lon}, \text{by} = x)$$

where `lat` and `lon` are vectors of the latitude and longitude (which could be replaced by other spatial coordinates) for each sample y , and x is the covariate with a spatially varying response. Alternatively, other software treats spatially varying intercepts and slopes (α_s and β_s , respectively) as random

effects. In such cases, an analyst must consider either 1) estimating a covariance between α_s and β_s , or 2) centering the covariate $x_i - \frac{1}{n_i} \sum_{i=1}^{n_i} x_i$, such that α_s and β_s have minimal covariance.

Seven ecological applications of SVCs

We identify seven circumstances in which SVCs increase model fit and result in more detailed and nuanced descriptions of ecological processes relative to conventional SDMs (Table 1). These are:

1. *Ecological teleconnections.* Local conditions and species densities are influenced by broader patterns of climatic links at geographically distant regions on various time scales. These ‘ecological teleconnections’ can sometimes explain variation beyond what is attributable to local habitat (Thorson 2019a). For example, changes in regional indices such as the El Niño Southern Oscillation cause variations in local density for skipjack tuna, *Katsuwonus pelamis* (Lehodey et al. 1997), such that local densities will have a spatially varying response to this oceanographic variable.
2. *Density-dependent habitat selection.* Many models of habitat selection result in animals changing their spatial distribution as total abundance increases (Avgar et al. 2020). For example, density-dependent habitat selection can

result in local responses to population abundance that vary across space (MacCall 1990). In many cases, this effect can be approximated by estimating a spatially varying response of local density to median or average population abundance, where a positive response indicates a faster-than-proportional increase in local abundance during population increases (Thorson 2022).

3. *Spatially varying detectability.* Local habitat conditions impact sampling performance. Sampling rarely identifies all individuals that are present at a given location, and local habitat conditions may substantially increase or decrease the probability of sampling each individual. In fishes, for example, increased primary productivity and a resulting decrease in water clarity decreases near-bottom light levels, which in turn decreases net herding and catchability in flatfishes (Ryer et al. 2010). In cases with paired sampling and local demographic closure (MacKenzie et al. 2002), it may be possible to estimate how detectability varies across space, and this will be necessary when the covariates affecting detectability (e.g. light levels) are unmeasured.
4. *Responses to missing covariates.* Habitat quality often arises from the interaction of multiple variables (e.g. metabolic demand and food availability), but when one of these variables cannot be measured directly, we may use spatially varying coefficients to quantify the impact of other variables across space. Context-dependent covariate responses can also represent a missing covariate; for example, two species that compete for the same food may have different

Table 1. List of ecological questions that can be addressed using spatially varying coefficients (‘Ecological question’, and also see ‘Seven ecological applications of SVCs’ subsection for more details), the variable that is spatially varying in each case (‘Variable’), three ways of classifying these questions by ‘Type’ (U: univariate; M: multivariate), ‘Covariate’ (C: continuous; I: indicator), and ‘Response’ (X: density; Q: catchability/detectability), and example references using VAST or other software. We illustrate the final three cases in detail in the main text.

Ecological question	Variable	Classification			Examples	
		Type	Covariate	Response	VAST	Other
Are there nonlocal features that cause predictable variation in local densities?	Regional climate indices	U / M	C	X	Thorson 2019a	Ciannelli et al. 2012
Do changes in total population abundance result in predictable changes in local density?	Time-series of total abundance	U / M	C	X	Thorson 2022	Bacheler et al. 2009
Does the ratio of expected occupancy or density measured by two sampling methods vary across space in a manner that is not predicted by available covariates?	Indicator variable for sampling gear	U / M	I	Q	NA	NA
Do expected responses to local environmental conditions vary across space, e.g. as caused by an interaction with a covariate that is not directly measured?	Local environmental variable	U / M	C	X / Q	NA	Hixon and Jones 2005
Are there trends in spatial distribution that arise at a defined temporal scale (e.g. decadal)?	Spline basis-expansion of time	U / M	C	X	In text (Fig. 2)	Barnett et al. 2021
What morphological, behavioral, or life-history features describe species-specific spatial distribution and resulting community assembly?	Species-specific trait values	M	C	X	In text (Fig. 3)	Ovaskainen et al. 2017
Do individuals of a given species that were born in the same year (i.e. a cohort) have distinct spatial distributions that can be tracked throughout their lives?	Cohort indicator variable	M	I	X	In text (Fig. 4)	NA

levels of dominance in different micro-environments (Fowler 1990).

5. *Decadal trends.* Distributions vary over long time intervals. Distributional shifts at many time intervals can be estimated efficiently within spatio-temporal SDMs (Barnett et al. 2021), and this can be generalized to estimate trends over any specified timeframe of interest.
6. *Trait-based habitat suitability.* Research seeks to measure how species traits allow different taxa to occupy different habitat types. This ‘fourth corner problem’ (Legendre et al. 1997) has been one motivation for the development of joint SDMs (Ovaskainen et al. 2017). The association between traits and spatial habitat utilization can be addressed by estimating a spatially varying response to species traits (e.g. maximum size or age, trophic level).
7. *Cohort effects.* Integral projection models (IPMs) seek to project population size and distribution based on information about how species stage influences vital rates. There is a growing literature on size-structured JSDMs (Kristensen et al. 2014, Cao et al. 2020), but these can be extended by simultaneously estimating how habitat utilization differs among individuals born in different years (termed ‘cohorts’).

These seven applications can be categorized into three general categories: nonlocal effects, multivariate responses, and missing variables (Table 1). In summary, there is a broad range of ecological questions that can be addressed by extending conventional SDMs to include spatially varying coefficients. We describe in detail three of these cases: 1) decadal trends, 2) trait-based habitat suitability, 3) cohort effects, and we demonstrate how disparate applications arise from a shared model structure, using a single, common statistical package (see Table 1 for papers demonstrating other applications).

Implementation using VAST

We demonstrate SVCs in univariate and joint SDMs in three ecological examples (decadal trends, trait-based habitat suitability, and cohort effects) using the vector autoregressive spatio-temporal (VAST) package (Thorson and Barnett 2017, Thorson 2019b) in R (www.r-project.org). The R-INLA package (Lindgren 2012) can also implement both SVCs and multivariate models (Palmí-Perales et al. 2019), although we use VAST to allow low-level manipulation of parameter constraints (as detailed below). We provide the minimal background for each model type and then explain how these three models are derived as nested submodels.

VAST is conceptually similar to a standard GLM, and involves defining linear predictors, a link function, and a distribution for the response. However, it differs by defining two linear predictors, π_1 and π_2 for every observation $i \in \{1, 2, \dots, n_i\}$ or extrapolation-grid $g \in \{1, 2, \dots, n_g\}$. For continuous data, these linear predictors are transformed by a bivariate link function to calculate encounter probabilities and predicted densities for each observation (to calculate the likelihood used to estimate parameters) or extrapolation-grid

(to calculate spatially aggregated estimates of ecological variables). For discrete data, by contrast, these predictors are transformed to calculate zero-inflation probabilities and the expected data for a counting process.

For each linear predictor, VAST fits to observations i and predicts densities at extrapolation-grids g across a continuous spatial domain $\{s_i, s_g\} \in \mathbb{R}^2$ and discrete time-intervals $t \in \{t_1, t_2, \dots, n_t\}$ for each category $c \in \{c_1, c_2, \dots, n_c\}$. We refer to models with a single response variable ($n_c = 1$) as a univariate SDM, and otherwise as a multivariate or joint SDM. Each linear predictor is decomposed into temporal main effects $\beta(c, t)$, spatial main effects $\omega(s, c)$, and spatio-temporal effects $\varepsilon(s, c, t)$. They additionally include the action of two types of covariates:

1. Density covariates $x(s, c, t, p)$, which are used in the linear predictor for both observations i and extrapolation-grids g , and therefore approximate processes that affect true underlying densities or variables.
2. Detectability covariates $q(i, k)$, which are only used in the linear predictor for observations i and not extrapolation-grids g . Detectability covariates therefore measure processes that affect sampling but do not reflect underlying densities, i.e. sampling gears or processes (e.g. time of day) that are ‘filtered-out’ when predicting densities.

We therefore obtain:

$$\pi_1(i) = \underbrace{\beta_1(c_i, t_i)}_{\text{Temporal variation}} + \underbrace{\omega_1^*(s_i, c_i)}_{\text{Spatial variation}} + \underbrace{\varepsilon_1^*(s_i, c_i, t_i)}_{\text{Spatio-temporal variation}} + \underbrace{v_1(s_i, c_i, t_i)}_{\text{Variation due to density covariates}} + \underbrace{\zeta_1(i)}_{\text{Variation due to detectability covariates}}$$

where π_2 is defined identically, although the interpretation of parameters may differ given the link-functions involved (see the VAST user manual for further details regarding each component). Our focus here is on the spatial slopes that are included in density and detectability covariates.

Regarding covariates affecting densities (‘density covariates’):

$$v_1(s_i, c_i, t_i) = \sum_{p=1}^{n_p} (\gamma_1(c_i, t_i, p) + \xi_1^*(s_i, c_i, p)) x_1(s_i, c_i, t_i, p)$$

where $x_1(s_i, c_i, t_i, p)$ is a four-dimensional array of n_p covariates that quantify variation in density for time t and location s where sampling occurred for observation i in category c . The spatially varying slope is $\gamma_1(c_i, t_i, p) + \xi_1^*(s_i, c_i, p)$, where $\gamma_1(c_i, t_i, p)$ is the average effect of density covariate $x_1(s_i, c_i, t_i, p)$ for category c and $\xi_1^*(s_i, c_i, p)$ has a mean of zero and represents spatial variation in that effect. If covariate p is specified as an SVC, VAST estimates spatially varying slopes at each location as:

$$\xi_1^*(c, p) \sim \text{MVN}(\mathbf{0}, \sigma_{\xi_1}(c, p) \mathbf{R}_1)$$

where $\sigma_{\xi_1}(c, p)$ represents the estimated standard deviation of spatial variation in covariate \mathcal{P} for category c , and we here define \mathbf{R}_1 to include the action of bivariate interpolation in the stochastic partial differential equation (SPDE) being used (Lindgren et al. 2011). We envision that analysts will not typically estimate the spatial term $\xi_1^*(s_i, c_i, p)$ without also estimating the mean effect $\gamma_1(c_i, t_i, p)$. However, exceptions may arise, e.g. when multiple categorical variables are included and a corner constraint requires that some values of $\gamma_1(c_i, t_i, p)$ be fixed at zero for others to be identifiable.

Finally, regarding covariates that affect the sampling process ('detectability' covariates):

$$\zeta_1(i) = \sum_{k=1}^{n_k} (\lambda_1(k) + \varphi_1^*(s_i, k)) q_1(i, k),$$

where $q_1(i, k)$ is an element of n_k covariates that quantify variation in catchability, $\lambda_1(k)$ is the estimated impact of detectability covariates on this linear predictor and $\varphi_1^*(s_i, k)$ is zero-mean spatial variation, where spatial variation in detectability is specified as follows:

$$\varphi_1^*(k) \sim MVN(\mathbf{0}, \sigma_{\varphi_1}(k) \mathbf{R}_1)$$

where $\lambda_1(k) + \varphi_1^*(s_i, k)$ is the slope for covariate k at location s_i .

Detailed case studies

Decadal trends

In our first case-study, we demonstrate how to generalize the 'local trends' model (Barnett et al. 2021) to describe local decadal trends. To do so, we specify a density covariate $x(s, c, t, p) = x(t, p)$ that is constant across space s to represent temporal trends. We use a univariate model for simplicity of presentation, and therefore drop notation for category c . The remaining dimensions are computed by modifying a spline basis-expansion of time t , such that covariates (and associated slopes) can be interpreted as representing smooth changes over time (see Supporting information). We then add a restriction that the spatial slope variance is equal for all components of the spline, $\sigma_{\xi_1}(p) = \sigma_{\xi_1}$.

We fit this model using bottom trawl survey data for arrowtooth flounder *Atheresthes stomias* in the eastern Bering Sea from 1982 to 2019. In the eastern Bering Sea, arrowtooth flounder increased rapidly in abundance during the 1980s and 1990s and slowly expanded its range to shallower depths along the Bering Sea slope. Then in the 2000s and 2010s, arrowtooth flounder rapidly expanded its range across the relatively flat Bering Sea continental shelf. We therefore fit an order-1 (i.e. linear) spline with four degrees of freedom, so that each component represents the decadal distribution relative to the long-term average.

Trait-based habitat suitability

We next demonstrate how to estimate the impact of species traits using joint SDMs. For 16 seafloor-associated fish ('groundfish') species in the Gulf of Alaska, we examined how spatial variation in species density is attributed to four traits: maximum age, temperature, trophic level, and maximum length (Supporting information). Estimating a local response to traits is a model-based approach to the 'fourth corner problem,' i.e. using measured species densities to identify what traits are suitable for different habitat types (Legendre et al. 1997, Brown et al. 2014). We fit all years of data without specifying any process that varies over time (i.e. using a 'static' SDM). As such, we specify density covariates that are constant across space and time, $x(s, c, t, p) = x(c, p)$, where \mathbf{X} is a matrix of life-history traits (columns) for each species (row), using four traits such that $\mathbf{x}(c) = \{\log(\max \text{ age}_c), \text{temperature}_c, \text{trophic level}_c, \log(\max \text{ length}_c)\}$. We center each trait (i.e. subtract traits by their mean value) to ensure that the trait-response maps $\xi_1^*(p)$ are uncorrelated with spatial components $\omega_1^*(c)$. We also scale each trait (i.e. divide each trait by its standard deviation) to ensure that $\xi_1^*(p)$ represents the response for a 'scale free' change in each trait. We then specify that spatial variation is identical across species, $\sigma_{\xi_1}(c, p) = \sigma_{\xi_1}(p)$, such that the estimated variance represents the magnitude of spatial response for each trait within a given community.

We apply this model to samples from a bottom trawl survey that was conducted in a stratified-random sampling design every three years from 1984 to 1999 and every two years from 2001 to 2019 in the Gulf of Alaska. We extract biomass for each of 16 groundfish species and species traits from an updated version of FishLife (Thorson 2020), a multivariate, phylogenetic trait-imputation model fitted to output from FishBase (Froese 1990). We do not estimate biomass dynamics over time, i.e. $\beta_1(c, t) = \beta_1(c)$ and $\varepsilon_1(s, c, t) = 0$, and specify zero-centered trait responses, i.e. $\gamma_1(c, p) = 0$, to avoid confounding between $\beta_1(c)$ and the mean of covariates. We then visualize the estimated response maps $\xi_1^*(p)$ to identify the geographic areas that are associated with each trait. These maps identify locations where a given trait is expected to have higher density, e.g. a response of $\xi_1^*(s, p) = 0.1$ indicates that a species with one standard deviation higher value for trait p is expected to have 10% higher density than at a location where $\xi_1^*(s, p) = 0$.

Cohort effects

Finally, we demonstrate how to estimate cohort effects in an age-structured (multivariate) spatio-temporal model. Cohort-specific spatial distribution has previously been documented for walleye pollock *Gadus chalcogrammus* in the Bering Sea (Stevenson et al. 2022), but no study has visualized the spatial map specifically associated with each cohort. We specify that density covariates $x(s, c, t, p)$ are constant across space and follow a banded indicator matrix across ages c and years t :

$$x(c, t, p) = \begin{cases} 1 & \text{if } t + n_c - c = p \\ 0 & \text{otherwise} \end{cases}$$

while restricting $\xi_i^*(s, c, p) = \xi_i^*(s, p)$ and a common variance for all cohort-response maps, $\sigma_{\xi_i^*}(c_i, p) = \sigma_{\xi_i^*}$. This results in the following correspondence between $\xi_i^*(p)$ and cohort or year order:

$$\xi_i^*(c, t) = \begin{bmatrix} \xi_i^*(n_c) & \cdots & \xi_i^*(1) \\ \vdots & \ddots & \vdots \\ \xi_i^*(n_c + n_t) & \cdots & \xi_i^*(n_c) \end{bmatrix}$$

where we visualize $\xi_i^*(p)$ for selected cohorts, as well as $\xi_i^*(c, t)$ for the full matrix of ages and years.

Model evaluation

For each case study, we evaluate performance of the SVC model via a comparison with the same model without SVCs. We compare performance in three ways:

1. *Parsimony.* We calculate the marginal Akaike information criterion (Akaike 1974), and use the difference in AIC as an estimate of predictive error when balancing bias and imprecision ('parsimony');
2. *Variance explained.* We calculate the percent deviance explained (PDE), conditional upon empirical Bayes predictions of random effects. This involves calculating the deviance of 'saturated' and 'null' models; we interpret the latter as a model with a separate intercept and measurement variance parameter for each category c .
3. *Descriptive power.* Finally, we visualize and use subject-matter expertise to provide ecological interpretation for the estimated SVC and use this to highlight the potential for SVC to add nuance and detail to the resulting description of ecological processes.

The first two performance metrics reflect quantitative aspects of statistical performance, whereas the latter reflects qualitative improvements in ecological learning (see the Supporting information for code to replicate all three case studies).

Results

Based on statistical performance metrics, we see mixed support for the models with or without SVC (Table 2). In particular, AIC shows that the models with an SVC are more parsimonious (i.e. expected to improve predictive performance) but also have a negligible decrease in deviance explained relative to the model without an SVC. Given this mixed statistical support, we emphasize in the following the benefits of including an SVC in terms of greater ecological nuance and descriptive power.

The decadal trends model highlights that Bering Sea arrowtooth flounder densities in 1982 are highest in the outer domain (the western boundary of the eastern Bering Sea, top-left panel of Fig. 2). From 1982 to 1994, increases in density are proportional throughout the Bering Sea (Fig. 2,

Table 2. Comparison for three case studies of models (rows) with or without spatially varying coefficients (SVCs), comparing parsimony ΔAIC (the difference in the marginal Akaike information criterion) and variance explained PDE (the percent deviance explained, calculated as the deviance relative to a saturated or null model).

Case study	Parsimony ΔAIC		Variance explained PDE	
	No SVC	SVC	No SVC	SVC
Decadal trends	153.4	0.0	77.9%	77.6%
Trait-based habitat suitability	250.9	0.0	30.2%	30.1%
Cohort-specific spatial distribution	376.3	0.0	66.5%	66.5%

top-right panel), while densities increase in hotspots north of Unimak Pass or Zhemchug Canyon from 1994 to 2007 relative to other areas (Fig. 2, bottom-left panel). However, the trend from 2007 to 2019 is striking, with relatively large increases in density in the northern portion of the eastern Bering Sea (Fig. 2, bottom-right panel). Total abundance increased fastest from 1982 to 2005 (Supporting information), so the distribution shift northward from 2007 to 2019 is largely distinct from the increased abundance seen during previous decades (Supporting information).

In the trait-based joint SDM, we attribute spatial variation in the density of 16 groundfish species to four traits: maximum age, temperature, trophic level, and maximum length (Fig. 3). The correlation among these traits is generally small, with the highest correlation (0.45) between log (maximum length) and trophic level (Supporting information). The joint SDM identifies a variance approaching zero for trophic level, suggesting that this trait is not parsimonious in describing community distribution. The effect size ($\sigma_{\xi_i^*}^2(p) \text{Var}(\mathbf{x}_p)$) is highest for temperature, which shows a decreased density for warm-associated species in the western Gulf of Alaska, specifically near Unimak Pass, and elevated densities from Kodiak Island eastward. Meanwhile, long-lived species tend to have higher densities near the continental shelf-break (i.e. at the southern boundary of the bottom trawl survey) and large-bodied species tend to have elevated densities on the continental shelf west of Kodiak Island. We therefore conclude that temperature, body size, and maximum age shape community assembly for demersal fishes in the Gulf of Alaska.

In the cohort analysis, we identify several cohorts of Bering Sea pollock whose spatial distributions are distinct from the long-term average (Fig. 4). For example, 1981 and 1986 cohorts show density hotspots in the outer region of the continental shelf, with higher densities either in the south (1981) or the north (1986). By contrast, 1996 and 2009 cohorts are distributed more evenly throughout the Bering Sea shelf, though the 2009 cohort has proportionally higher densities in the northern portion. Finally, 2002 and 2015 cohorts showed considerably higher concentrations of pollock in the northwest and northeast portions of the Bering Sea, respectively. The 2002 cohort has a distribution in the northern portion of the middle shelf that is noticeable from 2007 to 2012 (i.e. ages 5–10, Supporting information). Similarly, the 2009 and

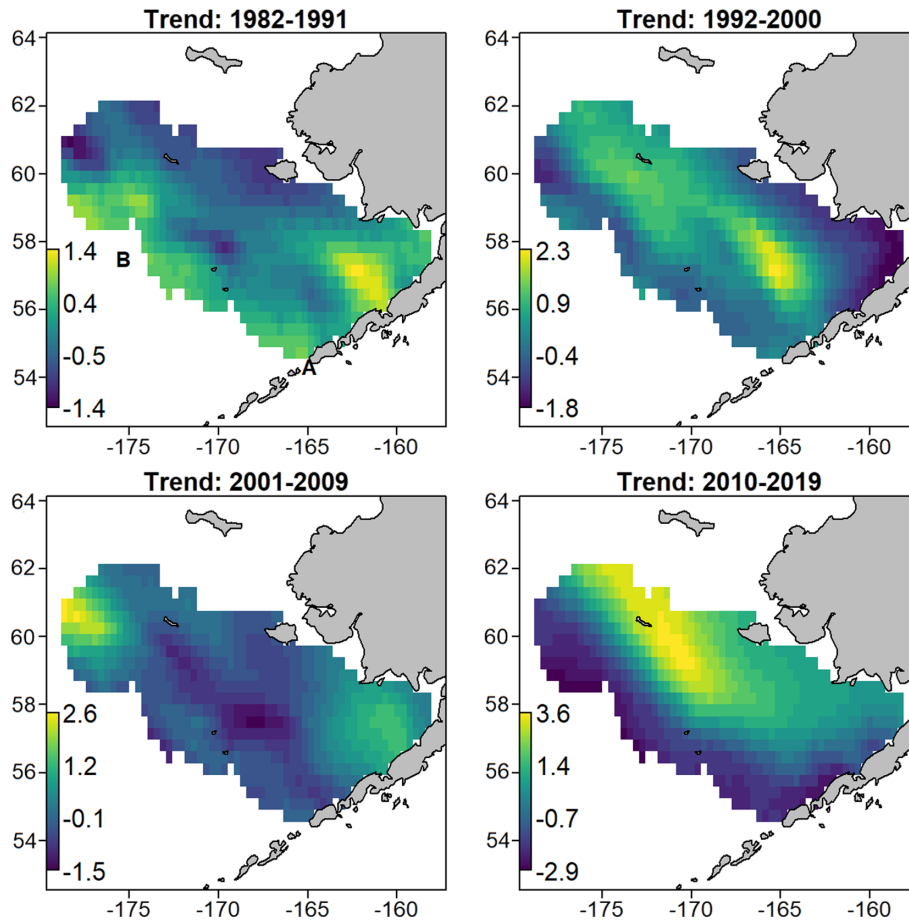


Figure 2. Results from the ‘decadal trends’ model fitted to abundance data for arrowtooth flounder in the eastern Bering Sea, with black labels (top-left panel) indicating Unimak Pass (‘A’) and Zhemchug Canyon (‘B’), and showing the trend in log-density during four intervals from 1982 to 2019 (see panel labels for year ranges), where e.g. a value of 0.1 in the bottom-right panel would indicate that a location had an approximately 10% increase in abundance from 2010 to 2019 (after controlling for interannual changes in total abundance). These response maps are multiplied by the I-spline basis expansion of years (Supporting Information) to generate the covariance-response function.

2015 cohorts can easily be tracked through time by plotting densities by age class and year (Supporting information).

Discussion

In this paper, we introduced the statistical theory and software for fitting SVCs and reviewed seven common ecological applications where SVCs could be relevant. We then compared the performance of SDMs with or without SVCs in detail using three novel case studies, on the basis of statistical performance (parsimony and deviance explained) or improved ecological interpretation. In this discussion, we summarize lessons learned from this comparison before recommending that ‘good practice’ guidance for SDM development emphasize the value SVCs when evaluating multiple hypotheses for shifting spatial distributions.

On a purely statistical basis, we saw mixed support for the inclusion of SVCs relative to SDMs without them. In all three case studies, marginal AIC identified a substantial (>10

ΔAIC) improvement from including SVCs. Given that the models with and without SVCs are nested, this result implies that the SVCs are also ‘statistically significant’ on the basis of a likelihood-ratio test. We interpret AIC as a simple form of model regularization (Hooten and Hobbs 2015), in this case shrinking variance parameters to exactly zero. We note that estimating SVCs as a Gaussian random field (as we do here) involves an additional shrinkage of variance parameters towards zero. In fact, estimating an SVC variance at zero due to shrinkage during parameter estimation occurred in the second case study (‘trait-based habitat suitability’), confirming that SVCs will revert to a simpler model structure when data suggest that doing so is parsimonious. Given this shrinkage during parameter estimation, it is unsurprising that marginal AIC generally identifies SVCs as parsimonious. We recommend further research to improve access to conditional AIC as an alternative model-selection metric that penalizes random effects more strongly (Grevén and Kneib 2010). Despite this improved parsimony, the model with SVCs show a negligible decrease in percent-deviance-explained (when calculated

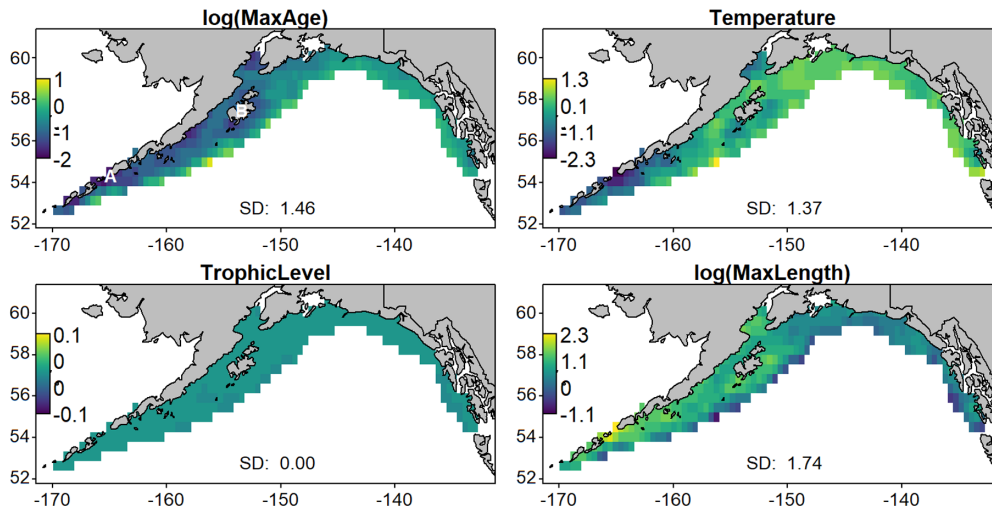


Figure 3. Results from the ‘trait-based habitat suitability’ model, showing the impact of four traits (panels) on expected log-density for 16 groundfishes in the Gulf of Alaska, with white labels (top-left panel) indicating Unimak Pass (‘A’) and Kodiak Island (‘B’). Traits are standardized (i.e. have a unit variance) prior to analysis, such that a value of 0.1 at location s indicates that a species c_1 with a trait value that is one standard deviation above the average is expected to have a 10% increase in density relative to a species c_2 with an average value for that trait. Note that the color range differs among plots to highlight spatial patterns for each trait. The spatial standard deviation (SD) is listed at the bottom of each panel.

using empirical Bayes estimators of random effects) and has essentially no impact on model residuals. In each case study, the SVC is used to describe a type of variability that is otherwise attributed to an estimated spatial (i.e. for trait-based habitat suitability) or spatio-temporal random field (i.e. for decadal trends or cohort effects). We therefore see that the models with or without SVC will both converge asymptotically on the same estimates of density (Klein 1976), but their statistical performance will differ for a finite sample size. The small impact on percent-deviance-explained is in line with other recent studies (Brodie et al. 2020). We hypothesize that the empirical Bayes estimator of SVCs may show improvements in percent-deviance-explained for smaller sample sizes than those used here, but leave this comparison as a topic for future statistical research.

In contrast to the mixed statistical support, we see unequivocal benefits to including SVCs in terms of improved ecological description. In the three detailed case studies (as well as the four applications discussed without illustration), estimating an SVC allows description of an ecological process that otherwise remains latent. These latent processes could perhaps be extracted from the model without SVCs by performing some ‘statistics on statistics’ (i.e. averaging various estimated variables), but this precludes evaluation of statistical performance. Using SVCs to integrate regional environmental covariates, life-history traits, and phylogenetic relationships within SDMs can provide an avenue to test theoretical predictions about community assembly and evolution, and illuminate ecosystem dynamics across broader temporal scales. As seen in the third case study, SVCs can also identify mechanisms that drive distributional change (Pinsky et al. 2020) and be adapted to examine impacts from short-term events like heatwaves (Jacox et al. 2020). SVCs

offer the potential to incorporate a wide range of hypotheses about climate responses, including trait-mediated, cohort-specific, and local responses to regional conditions.

The addition of SVCs to species distribution models provides a way to account for multiple explanations for spatial distribution within a single modeling framework, while allowing for model comparison on the basis of statistical performance or improvements in ecological understanding. Commonly used SDMs tend to relate local density to local environmental drivers and may inadvertently attribute regional effects to local drivers or otherwise fail to identify important covariates when they have a response that varies spatially (Heim et al. 2021). This limits the predictive abilities of SDMs, making them less useful tools for addressing widespread ecological change. Conversely, aggregating data at inappropriate spatial scales can lead to a mischaracterization of statistical relationships or dampen finer-scale variation in favor of broader-scale processes. Traits like dispersal mode and migration status, for instance, may represent important life-history strategies that exhibit regional variation and impact local species distributions. Studies have shown that traits which encourage long distance travel (e.g. mobile pelagic larvae, migratory capacity of adults) might be overrepresented in regions that are subjected to high levels of disturbance (Smale 2008). In addition to trait data and environmental variables, phylogenies could also be treated with a spatially varying response to examine macro-level trends in community dynamics. For example, communities commonly exhibit phylogenetic clustering, whereby closely-related species tend to have similar or overlapping spatial distributions (Ives and Helmus 2011) but the degree of phylogenetic signal can vary across latitudes (Spalink et al. 2018) or environmental gradients (Mienna et al. 2020). Thus, ecologists need analytical

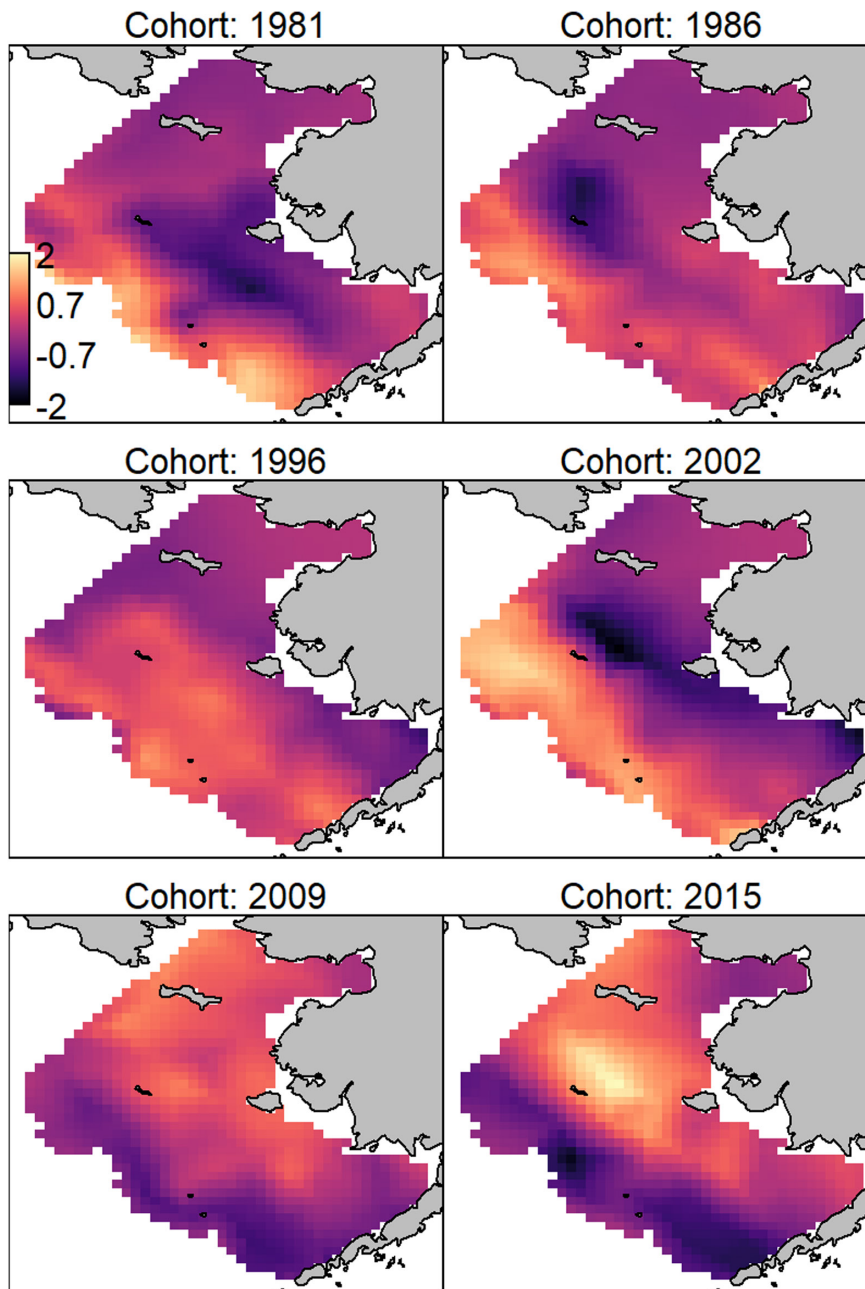


Figure 4. Results from the ‘cohort effects’ model for Bering Sea pollock, showing the partial effect of cohort, i.e. the log-ratio of density relative to the long-term average density at each location for a cohort born in year 1981 (top left) through 2015 (bottom right). Note that panels have the same scale to emphasize differences in the magnitude of cohort-specific density across cohorts.

tools that can account for multiple hypotheses, including both fine- and broad-scale processes when characterizing ecological processes (Turner et al. 1989).

Many previous papers have reviewed or recommended ‘best practices’ for SDMs. Several authors describe theoretical considerations for model building and recommend specific techniques for evaluating model performance (Guisan and Zimmermann 2000, Araújo and Guisan 2006, Petitpierre et al. 2017, Winship et al. 2020). Others generate SDM guidance by comparing the relative skill of

different modeling frameworks (Segurado and Araújo 2004, Knudby et al. 2010, Robinson et al. 2011, Duan et al. 2014, Norberg et al. 2019). SVCs, however, are largely missing from discussions about SDM best practices, even among papers that exclusively focus on the treatment of spatial processes (Dormann et al. 2007, Commander et al. 2022). Geographically weighted regression (GWR) and spatial filtering have been introduced as ways to deal with non-stationarity (Austin 2007, Martínez-Minaya et al. 2018), though SVCs have been found to perform better (Gelfand et al. 2003,

Finley 2011). SVC models also allow for complicated dependencies rather than modeling responses to a spatial average of nearby conditions, either by smoothing covariates or estimating a kernel smoother during model fitting (Chandler and Hepinstall-Cymerman 2016). For these reasons, we encourage the incorporation of SVCs into guidance documents as a way of familiarizing SDM users with their various benefits and applications, and to promote their inclusion during model exploration, selection and ensemble formation.

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Author contributions

James T. Thorson: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Cheryl L. Barnes:** Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Sarah T. Friedman:** Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Janelle L. Morano:** Resources (equal); Writing – original draft (equal); Writing – review and editing (equal). **Margaret C. Siple:** Resources (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available in R-package VAST (<https://github.com/James-Thorson-NOAA/VAST>) release $\geq 3.10.0$, and can be accessed after installing and loading the package using `'data(arrowtooth_trends)'`, `'data(goa_traits)'`, or `'data(pollock_cohorts)'`, with descriptions available via e.g., `'?arrowtooth_trends'`

Supporting information

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

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