

RESEARCH ARTICLE

Dynamic structural equation models synthesize ecosystem dynamics constrained by ecological mechanisms

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Email: james.thorson@noaa.gov**Funding information**

National Science Foundation, Grant/Award Number: OCE-1538582

Handling Editor: José Miguel Ponciano**Abstract**

1. Ecological analyses typically involve many interacting variables. Ecologists often specify lagged interactions in community dynamics (i.e. vector-autoregressive models) or simultaneous interactions (e.g. structural equation models), but there is less familiarity with dynamic structural equation models (DSEM) that can include any simultaneous or lagged effect in multivariate time-series analysis.
2. We propose a novel approach to parameter estimation for DSEM, which involves constructing a Gaussian Markov random field (GMRF) representing simultaneous and lagged path coefficients, and then fitting this as a generalized linear mixed model to missing and/or non-normal data. We provide a new R-package *dsem*, which extends the 'arrow interface' from path analysis to represent user-specified lags when constructing the GMRF. We also outline how the resulting nonseparable precision matrix can generalize existing separable models, for example, for time-series and species interactions in a vector-autoregressive model.
3. We first demonstrate *dsem* by simulating a two-species vector-autoregressive model based on wolf–moose interactions on Isle Royale. We show that DSEM has improved precision when data are missing relative to a conventional dynamic linear model. We then demonstrate DSEM via two contrasting case studies. The first identifies a trophic cascade where decreased sunflower starfish has increased urchin and decreased kelp densities, while sea otters have a simultaneous positive effect on kelp in the California Current from 1999 to 2018. The second estimates how declining sea ice has decreased cold-water habitats, driving a decreased density for fall copepod predation and inhibiting early-life survival for Alaska pollock from 1963 to 2023.
4. We conclude that DSEM can be fitted efficiently as a GLMM involving missing data, while allowing users to specify both simultaneous and lagged effects in a time-series structural model. DSEM then allows conceptual models (developed with stakeholder input or from ecological expertise) to be fitted to incomplete time series and provides a simple interface for granular control over the number of estimated time-series parameters. Finally, computational methods are

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sufficiently simple that DSEM can be embedded as component within larger (e.g. integrated population) models. We therefore recommend greater exploration and performance testing for DSEM relative to familiar time-series forecasting methods.

KEYWORDS

causal model, graphical model, qualitative network model, simultaneous equation model, structural equation model, vector-autoregressive model

1 | INTRODUCTION

Ecological systems typically involve many interacting variables. Scientists typically seek to understand how these variables will change given a hypothetical policy, experimental manipulation or global change scenario. These predictions require understanding how a change in one variable will cause a subsequent change in another (termed 'causal analysis'). Causal analysis has motivated the development of a tremendous range of analytical techniques including structural equation, vector-autoregressive, instrumental variable and co-integration models (to name just a few).

Causal statistics in ecology and other disciplines is often interpreted using do-calculus (Pearl, 2009a). These methods involve defining a 'causal map', that is, a graphical model where variables are represented as boxes and causal mechanisms as arrows. Assuming that these mechanisms are all linear and all sampling units are statistically independent, the causal map then reduces to a structural equation model (SEM).¹ SEM has been studied for over 100 years (Wright, 1921, 1934) and debates continue about its relationship with alternative approaches to study causality (Bollen & Pearl, 2013). SEM can include latent variables for which no observation is available, and these might include composite variables representing general theoretical concepts for which no direct measurement is possible (Grace & Bollen, 2008). SEM can also clarify the circumstances when a given causal effect is estimable, and if not, what additional 'instrumental variable' might render it estimable (Bollen et al., 2022). If the specified structural equation does not include loops (i.e. a directed acyclic graph) or missing values, then it can be solved using a sequence of piecewise regressions. Piecewise regression is a common solution within ecological applications, for example, in the R statistical environment (R Core Team, 2017) using package *piecewiseSEM* for regression (Lefcheck, 2016) or *phylopath* for phylogenetic comparative methods (van der Bijl, 2018). However, piecewise regression cannot be fitted to data sets that include missing values, or in systems that include cyclic dependencies (i.e. causal loops).

Many methods for fitting SEM require the assumption that multiple independent observations are available for a given system, either across space, time, species or involving other forms of replication.

However, ecologists often deal with non-independent observations. Although ecologists are generally familiar with challenges posed by non-independence in terms of study design (Hurlbert, 1984), model validation (Roberts et al., 2017) or regression modelling (Brooks et al., 2017), fewer studies have discussed strategies to address non-independence when studying causality among multiple interacting variables (although see Ives (2022) for some discussion). To address this, Thorson et al. (2023) developed methods to address phylogenetic correlations when estimating evolutionary trade-offs using missing or incomplete data using SEM. However, their method is not easily extended to time-series analysis where system variables have both synchronous and lagged effects.

We seek to develop a general 'dynamic structural equation model' (DSEM) that flexibly integrates information from ecological time series, cope with missing or non-independent data, while also providing the opportunity to tailor the analysis based on ecological knowledge. To do so, we first introduce 'separable' SEMs that combine structural equations and correlations across space, time or species, and generalize these to include 'nonseparable' covariance resulting from specifying both simultaneous and lagged effects. We then introduce a novel and computationally efficient approach to parameter estimation for nonseparable DSEM, which involves constructing a Gaussian Markov random field (GMRF) and fitting this using a generic interface as a generalized linear mixed model (GLMM). We demonstrate this DSEM using a simulation experiment involving a bivariate vector-autoregressive model based on real-world predator-prey dynamics. We then apply the approach to a recently documented trophic cascade involving seastar wasting disease, and climate impacts on prey forage for a commercially important fish. Methods are available as an R-package *dsem* on the Comprehensive R Archive Network (CRAN) (<https://cran.r-project.org/web/packages/dsem/>) using release 1.0.0 (Thorson, 2023), using a simple 'arrow-and-lag' notation to specify structural linkages and with package vignettes available to showcase features.

2 | METHODS

Causal statistics in ecology and other disciplines typically involve several steps that define putative causal relationships, estimate dependencies among related variables and predict how each variable responds to changes in the others (Bollen & Pearl, 2013; Pearl, 2009a). The initial step defines a 'causal map', that is, a

¹We follow Pearl (2012) in using the term 'simultaneous equation model' synonymously and see that paper for more discussion.

graphical model where variables are represented as boxes and causal mechanisms as arrows. Assuming that these mechanisms are linear and data are available from multiple sampling units that are statistically independent, the causal map then reduces to a structural equation model (SEM). This SEM represents dependencies among a vector of variables \mathbf{x}_i , measuring x_{ij} at sampling unit $i \in \{1, 2, \dots, I\}$ for each variable $j \in \{1, 2, \dots, J\}$, for example, log densities at I sites for J species. The analyst specifies a set of simultaneous equations among variables, $\mathbf{x}_i = \mathbf{\Gamma}\mathbf{x}_i + \boldsymbol{\epsilon}_i$ where $\boldsymbol{\epsilon}_i$ is a J -length vector of residual (process) errors at site i and $\mathbf{\Gamma}$ is the $J \times J$ matrix of path coefficients. Path matrix $\mathbf{\Gamma}$ is composed of path coefficients γ_{j_2, j_1} , where value γ_{j_2, j_1} implies that changing variable x_{i, j_1} by amount Δ is expected to cause a change in variable x_{i, j_2} by $\gamma_{j_2, j_1} \Delta$. Assuming that exogenous variation $\boldsymbol{\epsilon}_i$ follows a multivariate normal distribution $\boldsymbol{\epsilon}_i \sim \text{MVN}(\mathbf{0}, \mathbf{\Lambda}\mathbf{\Lambda}^t)$, we can solve for the Cholesky of the process-error covariance $\mathbf{L} = (\mathbf{I} - \mathbf{\Gamma})^{-1} \mathbf{\Lambda}$ where $\boldsymbol{\Sigma} = \mathbf{L}\mathbf{L}^t$ is the expected $J \times J$ covariance $\text{Var}(\mathbf{x}_i)$ among variables across sampling units. SEM typically estimates parameters by calculating the sample variance \mathbf{S} among replicated observations. Conventional SEM then specifies a Wishart probability density $\mathbf{S} \sim \text{Wishart}(\boldsymbol{\Sigma}, I)$ for sample variance and maximizes this log density with respect to parameters (Kaplan, 2001).

Various research has then extended SEM to include non-independent observations. For example, Hershberger et al. (1996) proposed calculating a lagged covariance among measurements and then providing that as input to SEM-fitting software. Similarly, Cziráky (2004) proposed augmenting the SEM with lagged effects, reparameterizing all equations as a function of available observations and fitting that reparameterized model. These early approaches required complete data (no missing values). More recently, Asparouhov et al. (2018) fitted a generalized model including latent variables and missing data as a Bayesian hierarchical model, which they called 'dynamic structural equation models' (DSEM). This DSEM has been explored in several subsequent studies primarily in social sciences (e.g. McNeish & Hamaker, 2020). Relatedly, Thorson et al. (2023) applied a structural model for trade-offs among J species traits to calculate $J \times J$ trait-covariance $\boldsymbol{\Sigma}$. They then combined this with the evolutionary correlation among species represented using $I \times I$ matrix \mathbf{R} , derived from phylogenetic comparative methods. This specification resulted in a joint covariance among IJ traits and species calculated as the Kronecker product $\mathbf{R} \otimes \boldsymbol{\Sigma}$ of these two processes.

Importantly, ecological dynamics often arise from a combination of simultaneous and lagged effects among system variables. In marine ecosystems, for example, juvenile predators often compete with the same prey that they later consume as adults (Walters & Kitchell, 2001). Therefore, an increase in prey density can have a positive simultaneous effect (due to increased forage) and a negative lagged effect (due to decreased juvenile survival) on predators. In simple time-series extensions to SEM, we could define a $T \times T$ covariance \mathbf{R} over time and calculate the joint covariance $\mathbf{V} = \mathbf{R} \otimes \boldsymbol{\Sigma}$ from the time-series correlation \mathbf{R} and $J \times J$ covariance among variables $\boldsymbol{\Sigma}$. However, specifying different lags results in a covariance that cannot be represented as the Kronecker product of two smaller matrices, such that the precision matrix (the inverse of the variance/

covariance matrix) is nonseparable, and this necessitates expanding the computational machinery beyond those of Thorson et al. (2023).

Here, we define a matrix of time-series observations \mathbf{Y} where $y_{t,j}$ is the value in time $t \in \{1, 2, \dots, T\}$ and variable $j \in \{1, 2, \dots, J\}$, and we switch notation from I sites to T times to emphasize the time-series dependence among rows of \mathbf{Y} . We specify a GLMM:

$$\begin{aligned} y_{t,j} &\sim f_j(\mu_{t,j}, \boldsymbol{\theta}_j) \\ g_j(\mu_{t,j}) &= \alpha_j + x_{t,j} \end{aligned} \quad (1)$$

where f_j is a specified probability density for each variable where $\mathbb{E}(y_{t,j}) = \mu_{t,j}$ and given dispersion parameters $\boldsymbol{\theta}_j$, $g_j^{-1}(\alpha_j + x_{t,j})$ is the inverse-link transformation of a linear predictor that includes a mean α_j and variation $x_{t,j}$. We then specify GMRF for variation, $\text{vec}(\mathbf{X}) \sim \text{MVN}(\mathbf{0}, \mathbf{Q})$ where $\text{vec}(\mathbf{X})$ stacks the columns of the $T \times J$ matrix \mathbf{X} into a single vector with length TJ , and precision \mathbf{Q} is a $TJ \times TJ$ matrix that defines a distribution for $\text{vec}(\mathbf{X})$. In some cases, \mathbf{Q} is full rank (and therefore invertible) such that the covariance is calculated as \mathbf{Q}^{-1} and the distribution is proper, and in other cases, \mathbf{Q} is not full rank and the distribution for $\text{vec}(\mathbf{X})$ is improper. We emphasize that our notation allows intrinsic GMRFs where \mathbf{Q} is not full rank, for example, when specifying a random-walk process over time (Rue & Held, 2005 Chapter 3) or specifying that exogenous variance is zero for some variables a priori. GMRFs are a computationally efficient approach to represent the covariance arising from some hypothesized process that operates locally, such that \mathbf{Q} has many elements that are identical to zero (a 'sparse' matrix). Specifying a sparse precision \mathbf{Q} arises throughout modern statistics, for example, when modelling a spatially correlated variable by approximating spatial autocorrelation as local diffusion (Lindgren et al., 2011).

We start by extending the path notation (Wright, 1934) that is common in structural equation models. Using a bivariate ($J = 2$) example where $x_{t,1} = \mu_1 + \epsilon_{t,1}$ with intercept μ_1 and error $\epsilon_{t,1}$ and $x_{t,2} = \mu_2 + \gamma_{2,1}x_{t,1} + \epsilon_{t,2}$ defined similarly but where $\gamma_{2,1}$ is the slope linking $x_{t,1}$ and $x_{t,2}$, we could specify this succinctly in SEM arrow notation as $x_1 \leftrightarrow x_1; x_2 \leftrightarrow x_2; x_1 \rightarrow x_2$, and this can be parsed and fitted using standard R-packages (Fox, 2006; Fox et al., 2020). Extending this notation to include autocorrelation that differs between variables, we might instead specify the model $x_{t,1} = \mu_1 + \rho_1 x_{t-1,1} + \epsilon_{t,1}$ and $x_{t,2} = \mu_2 + \gamma_{2,1}x_{t,1} + \rho_2 x_{t-1,2} + \epsilon_{t,2}$ by extending arrow notation as $x_1 \leftrightarrow x_1; x_2 \leftrightarrow x_2; x_1 \rightarrow x_2; x_1 \rightarrow x_1(1); x_2 \rightarrow x_2(1)$, where the number in parentheses specifies the intended lag and this is not conventionally included in arrow notation for SEMs.

This expanded arrow notation allows us to represent a wide range of common ecological models including vector-autoregressive models (VARs), dynamic factor analysis and structural equation models with a separable time-series autocorrelation (Figure 1). For example, VARs typically estimate a $J \times J$ matrix \mathbf{B} that includes J^2 pairwise and lagged interactions (Ives et al., 2003). However, VARs do not typically estimate contemporaneous interactions (i.e. the coefficient γ_{x_2, x_1} in the previous example). Instead, VARs capture contemporaneous effects via an estimated covariance matrix that does not have the mechanistic interpretation of SEMs and therefore does

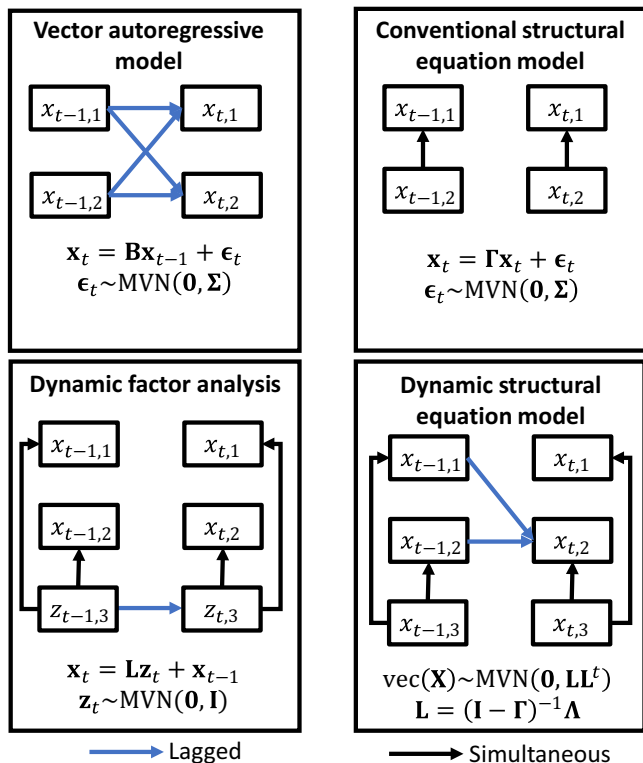


FIGURE 1 Graphical representation of a bivariate time-series model describing log abundance for a resource $x_{t,1}$ and consumer $x_{t,2}$ species, represented as vector \mathbf{x}_t in each time t . Dynamics could be represented using a vector-autoregressive (VAR) model with lagged interaction matrix \mathbf{B} (top-left), a conventional structural equation model (SEM) applied to each time with path coefficients $\mathbf{\Gamma}$ (top-right), or a dynamic factor analysis (DFA) with loadings matrix \mathbf{L} (bottom-left). The VAR assumes that all interactions are lagged, the SEM assumes that interactions are simultaneous, and the DFA estimates simultaneous associations while prespecifying a random walk for latent variable(s) \mathbf{z}_t . We introduce dynamic structural equation models (DSEM) which can include any combination of lagged and simultaneous effects among both original and/or latent variables, expressed via joint path matrix $\mathbf{\Gamma}$ and used to construct the precision of a Gaussian Markov random field. This DSEM is specified using an ‘arrow-and-lag’ notation and includes VAR, SEM, DFA and customized variants as nested submodels. Parameters are then estimated for all models by specifying an additional measurement process $\mathbf{y}_t \sim \text{MVN}(\mathbf{x}_t, \mathbf{V})$, although DSEM also allows a non-normal distribution for responses.

not lend itself to comparing the magnitude or statistical significance of simultaneous vs. lagged interactions. Syntactically, this only requires adding an extra column (for lags) to the standard ‘sem’ model specification (Fox, 2006).

Given this expanded arrow notation, we then convert a user-specified set of lagged and simultaneous effects to a joint path matrix $\mathbf{\Gamma}_{\text{joint}}$, which has dimension $TJ \times TJ$ where T is the number of years and J is the number of variables. Importantly, this matrix contains many zeros (i.e. is ‘sparse’) and is therefore computationally efficient to store and use. We also specify a variance σ_j^2 for independent exogenous variation for each variable and construct a nonseparable

$TJ \times TJ$ precision matrix, $\mathbf{Q}_{\text{joint}} = (\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^t \mathbf{V}^{-1} (\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})$ where $\mathbf{V} = \mathbf{I}_T \otimes \text{diag}(\boldsymbol{\sigma}^2)$, $\text{diag}(\boldsymbol{\sigma}^2)$ is the $J \times J$ diagonal matrix of exogenous variation σ_j^2 , \mathbf{I}_T is a $T \times T$ identity matrix. Importantly, we construct sparse precision $\mathbf{Q}_{\text{joint}}$ directly without having to construct or invert the covariance $\mathbf{Q}_{\text{joint}}^{-1}$ and then specify the probability density for the vector of observations, $\text{vec}(\mathbf{X}) \sim \text{MVN}(\mathbf{0}, \mathbf{Q}_{\text{joint}})$. Any two elements x_{t_1, j_1} and x_{t_2, j_2} for which $\mathbf{Q}_{\text{joint}} = 0$ are then conditionally independent. This implies that the analyst must explicit declare any causal dependency via the ‘lag-and-arrow’ notation that defines the joint path matrix $\mathbf{\Gamma}_{\text{joint}}$. From a scientific perspective, this allows analysts to be explicit in specifying any lagged or simultaneous mechanisms operating among variables. These explicit assumptions can then be confronted with data, where they might then be rejected if two variables are then found to not be conditionally independent.

In some cases, we also estimate the effect of an exogenous intervention where some values of \mathbf{X} are changed to $\mathbf{X} + \Delta$, and where Δ is the $T \times J$ matrix of experimental changes that might represent a single pulse experiment (i.e. $\delta_{j,t} \neq 0$ for the single time t of an experimental manipulation) or an ongoing press experiment (i.e. $\delta_{j,t} \neq 0$ for all times after an experimental manipulation commences). We seek to predict how this intervention propagates across variables and through time via the estimated path coefficients $\mathbf{\Gamma}_{\text{joint}}$. To understand this effect, we note that $\mathbf{Q}_{\text{joint}}$ is the precision resulting from all variables \mathbf{X} being near their equilibrium. However, intervention Δ has the consequence that some variables deviate from this equilibrium. Specifically, this causes a first-order change in $\mathbf{\Gamma}_{\text{joint}} \text{vec}(\Delta)$ from equilibrium, with a subsequent second-order change in $\mathbf{\Gamma}_{\text{joint}}^2 \text{vec}(\Delta)$, such that an exogenous intervention Δ ultimately results in a change in $\sum_{k=1}^{\infty} \mathbf{\Gamma}_{\text{joint}}^k \text{vec}(\Delta) = (\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^{-1} \text{vec}(\Delta)$ across all variables (as long as $\mathbf{I} - \mathbf{\Gamma}_{\text{joint}}$ is invertible). This term $(\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^{-1}$ has many potential uses, for example, to predict the likely consequences of a press or pulse experiment (Bender et al., 1984) and is in fact called the Leontief matrix when evaluating policy interventions using input-output models having a similar structure in econometrics (Miller & Blair, 2022). In particular, ecologists sometimes estimate dynamics that arise when a system starts at an initial condition that is far from this equilibrium. To estimate an initial condition that is far from equilibrium, we therefore estimate a vector of fixed effect δ_0 corresponding to an exogenous intervention in the initial time. We then expand the second term of Equation 1 to be $g_j(\mu_{t,j}) = \alpha_j + x_{t,j} + (\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^{-1} \text{vec}(\Delta_0)$ where Δ_0 is a $T \times J$ matrix of zeros except that the row corresponding to the initial condition is replaced with δ_0 . This allows us to predict how an initial condition $\mathbf{x}_0 + \delta_0$ propagates across variables and through time following paths $\mathbf{\Gamma}_{\text{joint}}$ (see Appendix A for a detailed explanation in a simple example). $\mathbf{I} - \mathbf{\Gamma}_{\text{joint}}$ is typically sparse, so we use a sparse LU decomposition to compute the product $(\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^{-1} \text{vec}(\Delta_0)$ without forming $(\mathbf{I} - \mathbf{\Gamma}_{\text{joint}})^{-1}$ in memory, and this allows us to calculate the effect of Δ_0 even in models with many variables and/or times. Estimating initial conditions δ_0 requires that the term $\mathbf{I} - \mathbf{\Gamma}_{\text{joint}}$ is invertible, although there is no such restriction when initial conditions are not estimated.

The resulting model therefore represents all timest $t \in \{1, 2, \dots, T\}$ and variables $j \in \{1, 2, \dots, J\}$ in $T \times J$ matrix \mathbf{X} , which is specified as

resulting from a GRMF with sparse $TJ \times TJ$ precision matrix \mathbf{Q} . It then estimates parameters within a GLMM including (optionally) the net effect of initial conditions δ_0 . We integrate across random effects using the Laplace approximation as implemented in TMB (Kristensen et al., 2016), optimize the marginal likelihood to identify parameters specified in the expanded arrow notation and calculate standard errors using a generalization of the delta method (Tierney et al., 1989). Equation 1 shows that DSEM is a GLMM wherein the random-effect precision is constructed from user-specified (simultaneous and lagged) effects. The Laplace approximation is widely used to estimate GLMM parameters, for example, in packages *lme4* (Bates & Maechler, 2009) and *glmmTMB* (Brooks et al., 2017) and Bates (2011) notes that fitting a linear mixed model involves optimizing a quadratic discrepancy function, such that the Laplace approximation will be exact when data are normally distributed. Path parameters in Γ_{joint} are then identifiable thanks to the restriction that they are constant across time. Many authors have explored estimation methods for graphical models including SEM and Bayesian networks (e.g. Pearl, 2009b), but we cannot find reference to fitting a structural equation model that involves lagged effects using the computational efficiency of a GRMF within a generalized linear mixed effects model.

We validate the DSEM software by comparing parameter estimates (and standard errors) to alternative software using the following case studies:

1. Klein-1 macroeconomic model: We first apply DSEM to a multivariate data set using the Klein-1 model (Kleiber & Zeileis, 2008) that includes both simultaneous and lagged effects. This data set has no missing data and therefore can also be fitted using a dynamic linear model using R-package *dynlm* (Zeileis, 2019). DSEM results in nearly identical estimates and standard errors (see Appendix B). We also contrast DSEM using the Laplace approximation or MCMC for parameter estimation, the latter using STAN (Stan Development Team, 2023) via *tmbstan* (Monnahan & Kristensen, 2018). This confirms that the both methods result in similar parameter estimates.
2. Predator–prey dynamics: We next apply DSEM to a bivariate data set using a cross-lagged (a.k.a. vector-autoregressive) model. We specifically use real-world data for wolf–moose interactions on Isle Royale from 1959 to 2019, collected annually by the ‘Wolves and Moose of Isle Royale’ project (Vucetich & Peterson, 2012). This model includes only lagged effects, and there are no missing values, such that it can be fitted using using *dynlm*, R-package MARSS (Holmes et al., 2012) or R-package *vars* (Pfaff, 2008). DSEM again results in nearly identical estimates and standard errors (see Appendix C ‘Comparison with vector-autoregressive models’).

We therefore conclude that DSEM inherits the validation, asymptotic properties and simulation testing that has previously been applied to those model configurations that can also be fitted by alternative (less generalized) software. We therefore explore DSEM

performance given missing data, which is not easily fitted using either *dynlm* or *vars* packages.

2.1 | Simulation experiment

We first present results from a simulation experiment involving the bivariate vector-autoregressive model for Isle Royale moose and wolf interactions. This is represented using lag-and-arrow notation as $x_1 \rightarrow x_1(1)$, $x_1 \rightarrow x_2(1)$, $x_2 \rightarrow x_1(1)$ and $x_2 \rightarrow x_2(1)$. We first fit DSEM to samples of wolf and moose abundance on Isle Royale. We then use the S3 generic function *simulate.dsem* in package *dsem* to conduct a parametric bootstrap for each of 500 simulation replicates, while leaving all parameters at their estimated values and resampling the GRMF \mathbf{X} based on the precision \mathbf{Q} resulting from estimated coefficients using real-world data. We specifically explore a hypothetical scenario where wolves are sampled less frequently than moose, and drop data for wolves in half of the years (selected randomly without replacement). For each replicate, we then refit the model using *dsem* or *dynlm* and record the four pairwise interactions from each model. In this ‘missing data’ scenario, DSEM estimates missing values as a state-space model while *dynlm* drops the associated observations. Results are intended to demonstrate the benefits of jointly estimating missing values and pairwise interactions (i.e. accounting for missing data), and also to demonstrate the simulation capabilities provided by package *dsem*.

2.2 | Case studies

We also present results when analysing two real-world ecological data sets. These data sets were previously collected and publicly available, and did not require additional permitting. Our first involves a well-documented trophic cascade in marine kelp ecosystems (Steneck et al., 2002). In these ecosystems, sea urchins (*Strongylocentrotus* spp.) graze on large macroalgae such as kelp (*Macrocystis* sp.) and can reach high abundances and eliminate kelp canopies in the absence of predators. Urchins can sustain high abundances even in low food environments by reducing energy allocated to reproduction. In California coastal ecosystems, the primary urchin predators are the Sunflower Seastar (*Pychnopodia helianthoides*) and Sea Otter (*Enhydra lutris nereis*), but the former actively seek out urchins with high energy conditions associated with intact kelp forests (Smith et al., 2021a). *P. helianthoides* were decimated by the recent outbreak of seastar wasting disease, synchronously with the 2014–2016 marine heat wave in the Northeast Pacific Ocean (Harvell et al., 2019). The collapse of *P. helianthoides* caused California coastal ecosystems to switch from a kelp-dominated to crustose coralline algae-dominated ‘urchin barren’ system (Burt et al., 2018).

We re-analyse time series for four species (sunflower seastars, sea urchins, sea otters and kelp) at each of 12 different sites, representing $J = 4 \times 12 = 48$ variables over $T = 21$ years. Counts of seastars, sea urchins and kelp are averaged from 2 m \times 30 m transects

replicated at each site (Carr & Caselle, 2020) and available each year, while annual counts of sea otters are from a census conducted by the US Geological Survey (Hatfield et al., 2019). We analyse seastars densities (rather than their log density) because some sites have a value of zero in later years. We constrain path coefficients to be identical across sites and specify an impact of sea star densities on the log of urchin density, log-urchin densities on kelp and the log count of sea otters on kelp, for a total of three estimated path coefficients. We also estimate a different magnitude of first-order autoregression for each variable. This specification results in seven estimated structural parameters. We analyse data that are publicly available on Dryad (Smith et al., 2021b).

Our second case study estimates how physical variables and forage availability affects overwinter survival for Alaska pollock (*Gadus chalcogrammus*) in their first year of life in the eastern Bering Sea (EBS). Alaska pollock recruitment is affected by high mortality during their first winter, and juveniles prey upon large copepods and euphausiids during the preceding summer and fall (Hunt et al., 2011). Predator-prey dynamics in the EBS are driven by the size of the pool of cold (<2°C) waters near the seafloor in summer ('cold pool extent'), which is created by sea-ice production during the preceding winter (Stabeno et al., 2012). The cold pool then creates a thermal barrier to movement for predators from offshore winter spawning to onshore summer foraging habitats (Thorson et al., 2021).

We seek to estimate how climate affects the abundance of copepod and euphausiid forage, driving juvenile pollock consumption of these species and affecting subsequent overwinter survival and recruitment. To analyse this multicausal system, we compile winter sea-ice extent and summer Euphausiid densities from the 2022 eastern Bering Sea Ecosystem Status Report (Siddon, 2022 fig. 29 and 57), cold-pool extent from the R-package 'coldpool' (Rohan & Barnett, 2023), fall *Calanus* abundance and stomach-content samples for juvenile pollock from the Alaska Fisheries Science Center (Dave Kimmel, pers. comm.), and recruitment and spawning biomass from the 2022 stock assessment for Alaska pollock (Ianelli et al., 2022 Tables 24 and 26). Pollock are also cannibalistic, so we assume that changes in spawning biomass (SSB) have a linear impact on log recruits per spawner (logRPS). Estimating this linear effect is equivalent to parameter β a linear reparameterization of the Ricker stock-recruit model $R_t = \alpha S_t e^{-\beta S_t + \epsilon}$ where S is spawning biomass, R is recruitment, and ϵ is a process-error term. Forage abundance and consumption is measured intermittently, and this suggests an analysis such as DSEM that jointly interpolates missing values and estimates structural relationships.

3 | RESULTS

The simulation experiment shows the improved precision for estimated species interactions when jointly estimating structural parameters and missing values, relative to fitting a dynamic linear model that drops missing data (Figure 2). Using the parametric-bootstrap simulator and dropping half of the predator time-series

measurements, we see that root-mean-squared-error (RMSE) is lower using DSEM for all four interaction parameters. For predator (wolf) impacts on prey (moose), the RMSE is decreased by nearly half (0.17 using *dynlm* vs. 0.11 using *dsem*) and similarly for prey density-dependence (0.17 using *dynlm* vs. 0.086 using *dsem*). In this latter case, both models have access to a complete time series for prey abundance, such that the improvement using DSEM arises from better discriminating predation (the cross-lagged interaction) from density-dependence (autocorrelation).

Fitting a 'trophic-cascade' model to time-series data shows that decreasing sea star density by 0.1 (per 2m×30m transect) is expected to increase urchins to $100\% \times e^{-18.6 \times -0.1} = 640\%$ of their former density (Figure 3). An increase in log-urchin density is subsequently expected to decrease kelp densities, where both of these estimates are statistically significant using a two-sided Wald test. Finally, an increase in log count of sea otters is estimated to have a positive effect on kelp, although this effect is not statistically significant. We therefore conclude that replicated site samples are able to detect a significant and substantial 'trophic cascade' from sea stars through kelp densities.

Results for the Alaska pollock first-winter survival in the eastern Bering Sea confirm that sea-ice production has a positive effect on cold-pool extent, and a resulting positive effect on abundance for both large copepods and euphausiids (Figure 4). However, cold-pool extent has a larger effect on copepods than euphausiids, suggesting that copepods are a larger proportion of forage in cold than in warm years. Years with higher copepod densities also show significantly larger percentage of copepods in juvenile pollock stomach contents, while the impact of euphausiid densities on their consumption by juvenile pollock is not statistically significant (perhaps due to the less frequent data available for euphausiids). Finally, both copepods and euphausiids are predicted to have a positive effect on juvenile pollock survival (and subsequent cohort strength). Finally, these mechanisms are estimated jointly while imputing missing values for forage densities in unsampled years, based on their covariance with other available variables and over time (Figure 5).

4 | DISCUSSION

We have extended structural equation models for use in time-series analysis, which we call dynamic structural equation models DSEM (similar to Asparouhov et al., 2018). We also introduce an 'arrow-and-lag notation' that extends existing SEM notation and allows generic specification of contemporaneous and lagged effects. This arrow-and-lag notation allows for high-level model specification that combines conventional SEM (including conventional linear models, instrumental variables and path analysis) with time-series analysis (e.g. vector-autoregressive models and dynamic factor analysis), thereby uniting two widely used families of ecological model. Linear models and their extensions (GLMMs and generalized additive models) are perhaps the most widely used statistical method in ecology, but ignore the ecological relationship among covariates that result in

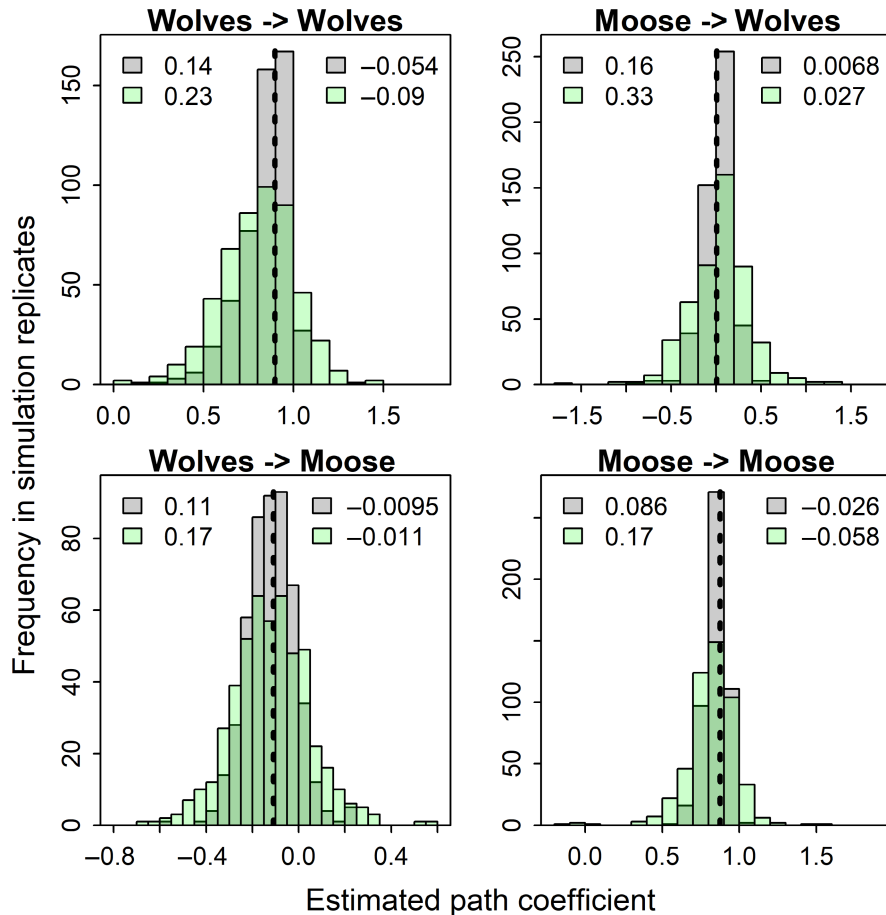


FIGURE 2 Estimated pairwise interactions from a simulation experiment fitting a bivariate vector-autoregressive model to wolf and moose abundance, showing estimates of the lagged interaction matrix **B** (labelled panels), with simulation-model parameters fixed at estimated values when fitting to real-world data from Isle Royale from 1959 to 2019 and data simulated given new realizations of the GMRF representing true log abundance using the *simulate* function in package *dsem*. We specifically compare estimates of four pairwise lagged interactions for each of 500 simulation replicates, fitted using *dsem* (grey) or *dynlm* (green) when data are missing for wolves in half of years, and showing the root-mean-squared-error (top-left) or bias (top-right) for each estimator.

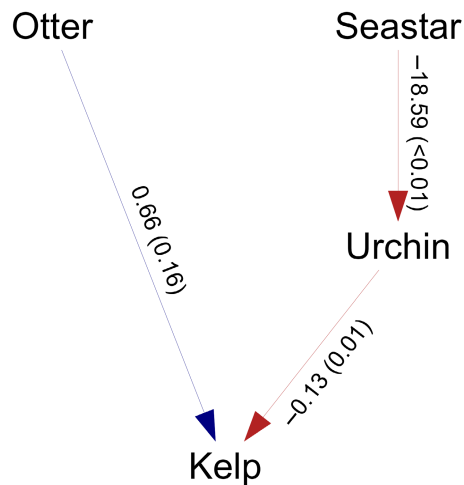


FIGURE 3 Estimated path diagram, showing variables (names) connected by path coefficients (numbers, listing the estimated value and the p-value from a two-sided Wald test in parentheses) for the trophic-cascade model fitted to time series for log-sea otter counts (Otter), sunflower seastar densities (Seastar), log-urchin densities (Urchin) and log-Kelp densities (Kelp). Note that the path coefficient estimates shown here are specified as identical across all 12 sites that are treated as separate time series for each species (48 time series total).

collinearity. This collinearity then causes poor model transferability (i.e. extrapolation in space or time) whenever the patterns of collinearity change (Dormann et al., 2013). We hope that the ‘arrow-and-lag’ notation improves the ease of use for SEM methods so that ecologists can apply structural modelling to explain collinearity within time-series analysis.

We then showed that DSEM can be specified using ‘arrow-and-lag’ notation, which is parsed to construct the sparse precision matrix for a GMRF, and this in turn is fitted within a GLMM. We first demonstrated how DSEM could fit a vector-autoregressive (a.k.a. cross-lagged) model for predator–prey interactions, and showed that jointly estimating interactions and missing data could improve statistical efficiency. We then demonstrated two ecological examples involving replicated measurements among sites (i.e. sea star trophic cascade), or multicausal attribution that includes lagged and simultaneous effects (i.e. forage and pollock recruitment). Our methods are available as R-package *dsem*, and we provide code and data to replicate these analyses as package vignettes.

One limitation of DSEM is that it assumes linear associations among variables. Methods are increasingly available to estimate non-linear causality among multiple variables in ecological systems. For example, convergent cross-mapping has been used to predict system properties in experimental settings (Deyle et al., 2016), although

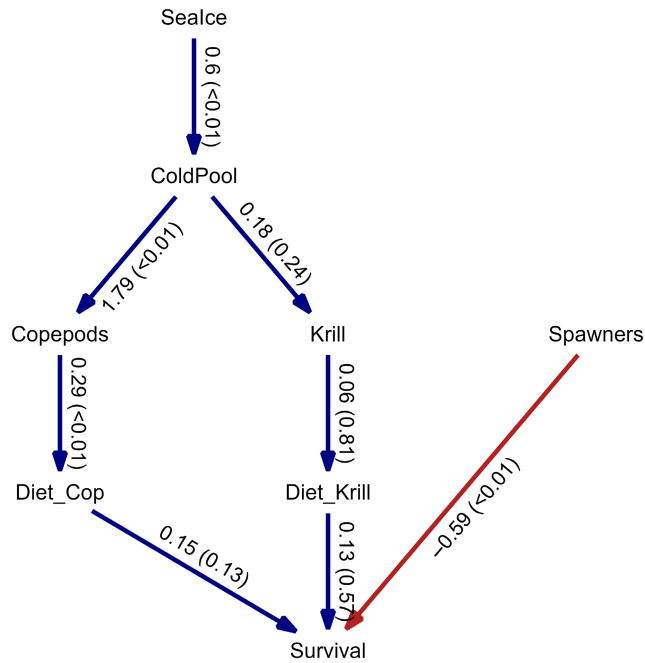


FIGURE 4 Estimated path diagram, showing variables (names) connected by path coefficients (numbers, listing the estimated value and the p -value from a two-sided Wald test in parentheses) for the eastern Bering Sea, involving log of winter sea-ice extent ('Sealce'), log of summer cold-pool extent ('ColdPool'), log-Euphausiid densities in the summer acoustic survey ('Krill'), log of large Calanus in the fall surface-trawl survey ('Copepods'), the average percentage of Euphausiids and copepods in age-0 pollock stomach samples in the fall surface-trawl survey ('Diet_Krill' and 'Diet_Cop', respectively), log recruits per spawners for Alaska pollock ('Survival') and spawning stock biomass for Alaska pollock ('Spawners').

debates continue regarding the performance of these methods (Chang et al., 2021; Yang et al., 2018). Similarly, nonparametric and nonlinear interactions have been estimated using artificial neural networks to approximate nonlinear differential equations (Bhat & Munch, 2022; Bonnaffé & Coulson, 2023). However, it is hard to incorporate a priori system knowledge within these nonparametric and nonlinear methods (although see Dolan et al. (2023) for progress involving convergent cross-mapping), and they typically require multiple generations to yield nonparametric estimates of the system attractor. Importantly, DSEM provides a simple and transparent interface to impose restrictions on system causality, for example, by restricting some potential linkages to be zero and constraining others to be constant over time. Alternatively, previous studies have argued that linearity (e.g. in vector-autoregressive models) can be usefully interpreted as approximating system dynamics around an equilibrium and have derived system-level properties from the resulting 'community matrix' (Ives et al., 2003; Wootton & Emmerson, 2005). We also note that other authors have incorporated interactions and nonlinearities within SEM (Holst & Budtz-Jørgensen, 2020; Schumacker, 2017), and we suspect that this is a feasible route to improve DSEM as well. For example, *piecewiseSEM* allows analysts to specify nonlinear responses within a non-recursive SEM. However,

interpreting nonlinear direct and indirect effects is challenging because the relationships are modelled as smoothing functions instead of linear coefficients, and *piecewiseSEM* is restricted to models with complete data and without loops (as stated previously). DSEM therefore reflects our belief that ecologists will continue to use a combination of linear and nonlinear methods for analysing interacting and multicausal systems.

One benefit of DSEM relative to nonlinear methods is that it has a simple user interface (i.e. the 'arrow-and-lag' notation) and can be specified using little logical code (i.e. parsing the 'arrow-and-lag' notation to construct the GMRF, and then fitting this in a GLMM). We therefore argue that DSEM can be repurposed as a modular component within larger bioeconomic models. For example, stock assessment models (SAMs) for fishes and integrated population models (IPMs) for wildlife typically require specifying a demographic model as 'motherboard' and then plugging heterogeneous data into this motherboard (Kéry & Schaub, 2021). These IPMs are often constructed to use covariates to explain or forecast demographic changes. However, this approach then ignores associations among available covariates, such that predictions may not represent the causal impact that includes both direct and indirect effects (Thorson, Hermann, Siwicke, & Zimmermann, 2021) and may not be transferable when patterns of collinearity change (Dormann et al., 2013). We therefore encourage further research that incorporates DSEM to represent associations among covariates within IPMs. For example, the model presented here for pollock recruitment could be incorporated directly within a state-space SAM, and this would allow fisheries managers to understand the direct and indirect impacts of climate change on this important commercial fishery.

In our presentation, we have emphasized a 'causal' viewpoint wherein DSEM is used to approximate structural linkages among interacting variables. However, causal inference will be biased when structural assumptions are mis-specified, either due to unknown mechanisms or unrecognized latent variables (Pearl, 2009b). We therefore note an alternative 'descriptive' viewpoint, wherein DSEM offers a pragmatic interface with granular control over the number of estimated parameters when describing covariance in a multivariate analysis. For C interacting variables, DSEM allows estimating from 1 to $C(C + 1)/2$ parameters while flexibly specifying restrictions among those. This DSEM specification expresses covariance using slope coefficients, which can then be compared with results from other descriptive regression models or easily communicated to researchers and stakeholders (Thorson et al., 2023). We recommend that researchers adapt this 'descriptive' interpretation whenever domain knowledge is insufficient to justify a causal interpretation of DSEM.

Calls are increasing to integrate local, traditional and Indigenous knowledge when developing ecological models that will be used for real-world management (e.g. Yua et al., 2022). We argue that causal maps represent a natural and intuitive way to solicit feedback from stakeholders about natural systems. Conceptual models are widely used to communicate system understanding (e.g. Wassmann et al., 2020 for Arctic ecosystems). Conceptual models

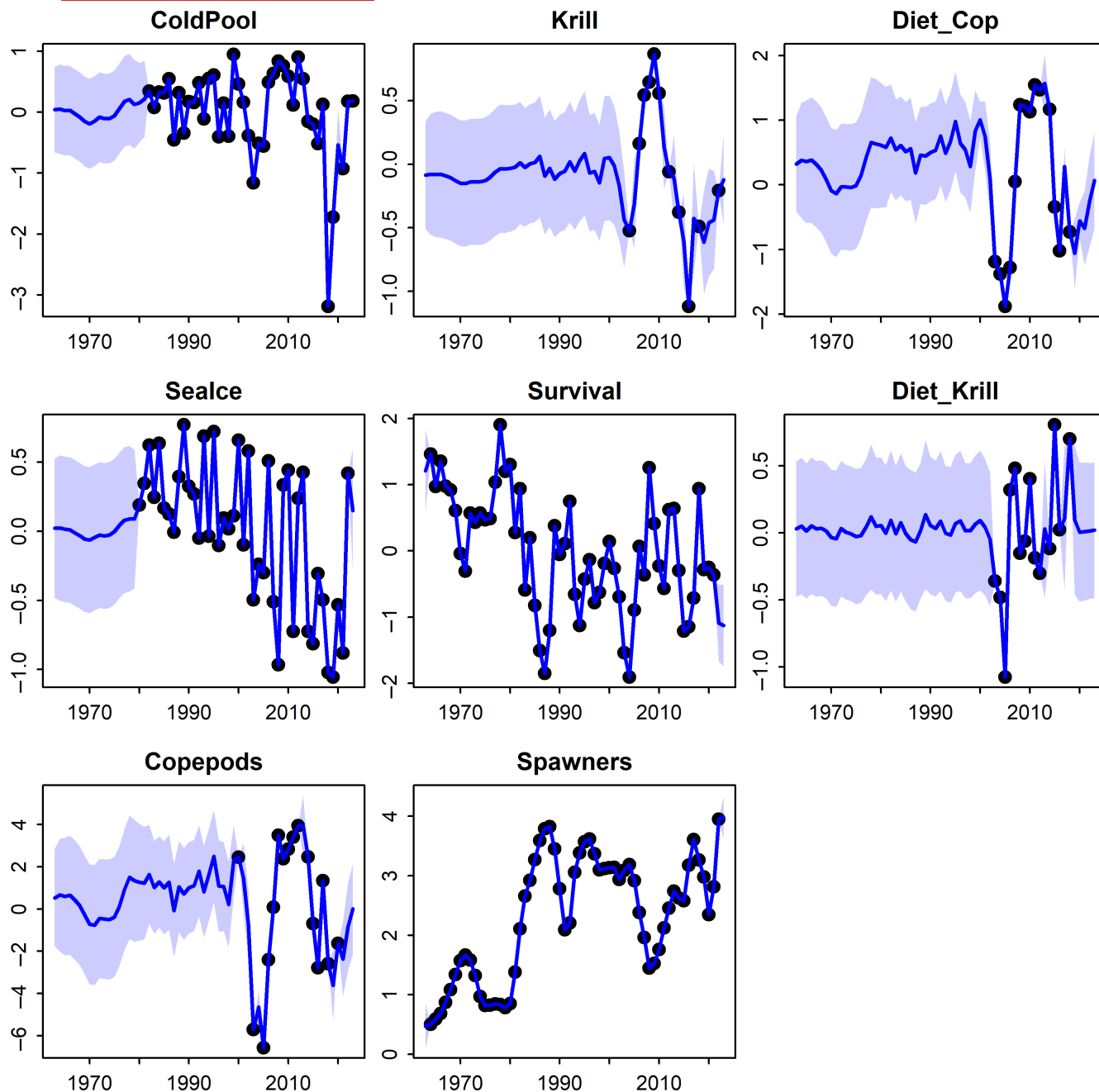


FIGURE 5 Estimated value for system variables in the eastern Bering Sea case study, showing eight variables (see [Figure 4](#) caption for definitions), showing measurements (black dots), predicted values (blue lines) and 95% predictive intervals calculated as ± 1.96 times the standard error.

that use boxes to represent variables and arrows to represent interactions can then be represented as a qualitative network model (Levins, 1974; Puccia & Levins, 1985), and Levins (1974) outlines how these can in turn be represented as a graphical model that approximates a set of nonlinear differential equations. We therefore argue that DSEM provides a convenient stepping stone to translate stakeholder input regarding contemporaneous or lagged drivers into a statistical model that can be fitted to noisy and incomplete data.

AUTHOR CONTRIBUTIONS

J. T. Thorson, T. E. Essington and S. I. Large discussed the issues regarding multicausal ecosystem drivers involving lagged and simultaneous effects. J. T. Thorson developed methods, wrote software, ran all analyses and led writing. T. E. Essington identified and curated the sea otter case study data. A. G. Andrews contributed to collecting, pre-processing and curating the Bering Sea case study data. All authors discussed and interpreted results and provided edits.

ACKNOWLEDGEMENTS

We thank E. Ward, E. Holmes and M. Scheuerell for previous discussions regarding vector-autoregressive models. We thank D. Kimmel for providing the copepod time series, P. Ressler for developing the euphausiid time series that we obtained from the Eastern Bering Sea Ecosystem Status Report led by E. Siddon, J. Ianelli for developing the assessment model estimating population biomass and recruitment, and L. Barnett and S. Rohan for developing the cold-pool index. We thank the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) at UC Santa Cruz for data used for the kelp forest trophic-cascade case study and acknowledge the NSF award (National Science Foundation grant OCE-1538582) that supported Smith et al. (2021a). We used published census and sea otter foraging data collected by the United States Geological Survey and Monterey Bay Aquarium. We thank K. Kristensen for developing Template Model Builder, without which this package *dsem* would not be feasible. Finally, thanks to S. Munch, K. Oke and two anonymous reviewers for helpful comments on a prior draft.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

For the Klein-1 case study (in the package vignettes), we analyse the version of these data provided by R-package AER (Kleiber & Zeileis, 2008). For the sea otter case study, we analyse data that are publicly available on Dryad (Smith et al., 2021b). For the eastern Bering Sea case study, we compile all data and include them as data set 'bering_sea' in the R-package 'dsem'. For the predator-prey data set, we analyse data for Wolf and Moose abundance from Isle Royale (Vucetich & Peterson, 2012), which are publicly available although we also include a static copy in package 'dsem'. Analyses can be reproduced using vignettes in R-package *dsem* release 1.0.0 (Thorson, 2023), available on CRAN (<https://cran.r-project.org/web/packages/dsem/>) or GitHub (<https://github.com/James-Thorson-NOAA/dsem>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Simple example of estimating initial conditions in a GMRF 12.

Appendix B. Additional figures and tables.

Appendix C. Demonstration of selected features.

How to cite this article: Thorson, J. T., Andrews, A. G. III, Essington, T. E., & Large, S. I. (2024). Dynamic structural equation models synthesize ecosystem dynamics constrained by ecological mechanisms. *Methods in Ecology and Evolution*, 15, 744–755. <https://doi.org/10.1111/2041-210X.14289>