

Regularizing priors for Bayesian VAR applications to large ecological datasets (#75686)

1

First submission

Guidance from your Editor

Please submit by **26 Aug 2022** for the benefit of the authors (and your \$200 publishing discount) .



Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



Raw data check

Review the raw data.



Image check

Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the [materials page](#).

7 Figure file(s)

1 Table file(s)



Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. BASIC REPORTING
2. EXPERIMENTAL DESIGN
3. VALIDITY OF THE FINDINGS
4. General comments
5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [Peerj standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [Peerj policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  All underlying data have been provided; they are robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.



The best reviewers use these techniques

Tip

Example

Support criticisms with evidence from the text or from other sources

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Regularizing priors for Bayesian VAR applications to large ecological datasets

Eric J Ward ^{Corresp., 1}, Kristin Marshall ², Mark Scheuerell ³

¹ Affiliate Professor, University of Washington, Northwest Fisheries Science Center, NMFS, NOAA, SEATTLE, WA, United States

² Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, Seattle, WA, USA

³ U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit, Seattle, WA, USA

Corresponding Author: Eric J Ward
Email address: eric.ward@noaa.gov

Using multi-species time series data has long been of interest for estimating inter-specific interactions with vector autoregressive models (VAR) and state space VAR models (VARSS); these methods are also described in the ecological literature as multivariate autoregressive models (MAR, MARSS). To date, most studies have used these approaches on relatively small food webs where the total number of interactions to be estimated is relatively small. However, as the number of species or functional groups increases, the length of the time series must also increase to provide enough degrees of freedom with which to estimate the pairwise interactions. To address this issue, we use Bayesian methods to explore the potential benefits of using regularized priors, such as Laplace and regularized horseshoe, on estimating interspecific interactions with VAR and VARSS models. We first perform a large-scale simulation study, examining the performance of alternative priors across various levels of observation error. Results from these simulations show that for sparse matrices, the regularized horseshoe prior minimizes the bias and variance across all inter-specific interactions. We then apply the Bayesian VAR model with regularized priors to the output from a large marine food web model (37 species) from the west coast of the USA. Results from this analysis indicate that regularization improves predictive performance of the VAR model, while still identifying important inter-specific interactions.

Regularizing priors for Bayesian VAR applications to large ecological datasets

Eric J. Ward*,¹

Kristin N. Marshall ²

Mark D. Scheuerell³

¹ Conservation Biology Division

Northwest Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

2725 Montlake Blvd. East

Seattle, WA 98112

² Fisheries Resource and Monitoring Division

Northwest Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

2725 Montlake Blvd. East

Seattle, WA 98112

³ U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit

School of Aquatic and Fishery Sciences

University of Washington

Seattle, WA 98105

* Corresponding author

Eric.Ward@noaa.gov

This draft manuscript is distributed solely for purposes of scientific peer review. Its content is deliberative and predecisional, so it must not be disclosed or released by reviewers.

Because the manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not represent any official USGS finding or policy.

33 Abstract

34 Using multi-species time series data has long been of interest for estimating inter-
 35 specific interactions with vector autoregressive models (VAR) and state space VAR models
 36 (VARSS); these methods are also described in the ecological literature as multivariate
 37 autoregressive models (MAR, MARSS). To date, most studies have used these approaches
 38 on relatively small food webs where the total number of interactions to be estimated is
 39 relatively small. However, as the number of species or functional groups increases, the
 40 length of the time series must also increase to provide enough degrees of freedom with
 41 which to estimate the pairwise interactions. To address this issue, we use Bayesian
 42 methods to explore the potential benefits of using regularized priors , such as Laplace and
 43 regularized horseshoe, on estimating interspecific interactions with VAR and VARSS
 44 models. We first perform a large-scale simulation study, examining the performance of
 45 alternative priors across various levels of observation error. Results from these simulations
 46 show that for sparse matrices, the regularized horseshoe prior minimizes the bias and
 47 variance across all inter-specific interactions. We then apply the Bayesian VAR model with
 48 regularized priors to a output from a large marine food web model (37 species) from the
 49 west coast of the USA. Results from this analysis indicate that regularization improves
 50 predictive performance of the VAR model, while still identifying important inter-specific
 51 interactions.

52

53

54 Key words: Bayesian lasso, spike-slab, regularization, shrinkage, VAR, VARSS, community

55 dynamics, multivariate regression, big data, variable selection.

Introduction

Across a wide range of statistical tools – ranging from simple linear regression to complicated spatiotemporal models – a fundamental question in ecology, fisheries, and related fields is identifying a subset of important predictor variables from a larger set of potential explanatory variables. These types of statistical analyses are often constrained by the "small n , large p " problem (West, 2003). For example, in basic linear regression analyses, the number of estimated parameters p cannot exceed the sample size n , because the degrees of freedom ($n - p$) is constrained to be greater than 0 (Zar, 1999). Furthermore, as p approaches n , the ability to estimate parameter uncertainty also diminishes. Similar constraints exist for hierarchical or mixed effects models, but calculating degrees of freedom becomes more complex (Spiegelhalter et al., 2002; Bolker et al., 2009).

Like other fields, ecology has recently undergone a "big data" revolution (Howe et al., 2008; Hampton et al., 2013b). Movement towards managing entire ecosystems rather than single species has spurred large-scale monitoring efforts and efforts to synthesize multiple associated data streams (Harvey et al., 2018). Simultaneously, greater ecosystem complexity has been incorporated in simulation models used for natural resource management (Sitch et al., 2003; Fulton, Smith & Johnson, 2003; Crowder & Norse, 2008). Regardless of whether inference is being made from observational data or simulation results, statistical models fit to these data may be challenged by the sample size. A classic example of a family of ecological models that has been limited by large streams of data are vector autoregressive (VAR) models (Hampton et al., 2013a). Ecologists use these models to estimate species interactions from observed multivariate time series (Ives et al., 2003; Holmes, Ward & Wills, 2012), and a general challenge of their use is that the number of

pairwise interactions in a community grows proportionately to the square of the number of species (Ovaskainen et al., 2017).

A number of dimension reduction approaches have been used in ecology and related fields to reduce many potential predictor variables to a subset of variables with high explanatory and predictive power. Popular examples include stepwise regression (Hocking, 1976) or all-subsets regression (Miller, 2002), and both are widely available in several R packages (R Core Team, 2021); examples include 'step' in *stats*, 'stepAIC' in *MASS* (Venables & Ripley, 2002), 'dredge' in *MuMIn* (Bartoń, 2020), and 'regsubsets' in *leaps* (Miller, 2020). Both stepwise and all subsets regression have widely documented shortcomings, including violating assumptions about multiple hypothesis testing (Whittingham et al., 2006; Mundry & Nunn, 2009) and the potential to identify spurious correlations (Olden & Jackson, 2000; Anderson et al., 2001), but they continue to be widely used.

In statistics, machine learning, and related fields, penalized regression has been used as an alternative technique to reduce model complexity (Hoerl & Kennard, 1970; Tibshirani, 1996; O'Hara & Sillanpää, 2009). Penalized regression consists of finding the combination of parameters that minimizes the objective function $g(\theta) = \sum_{i=1}^n (Y_i - \hat{Y}(\theta)_i)^2 + P$, where Y_i and $\hat{Y}(\theta)_i$ are the i^{th} observed and estimated data points, respectively; θ represents the regression coefficients; and P is a penalty term. For ordinary least squares regression, $P = 0$, and $g(\theta)$ reduces to the traditional sum of squares. Many choices for P exist, and are similar in that the further regression coefficients deviate from 0, the greater the penalty. One form known as ridge regression applies a quadratic or 'L2' penalty, $P = \lambda \sum_{j=1}^m \theta_j^2$, where λ is a shrinkage parameter that controls the degree of regularization (Hoerl & Kennard, 1970). A second approach, known as lasso regression (least absolute shrinkage

and selection operator), involves applying a 'L1' penalty of $P = \lambda \sum_{j=1}^m |\theta_j|$. For both ridge and lasso methods, as λ increases in magnitude, the penalty for the regression coefficients departing from zero also increases (Tibshirani, 1996). With many sparse coefficients, the advantage of using lasso regression is that absolute penalties of small values are greater than quadratic penalties, implemented in ridge regression (Wu & Lange, 2008). Thus, while lasso regression penalizes coefficients to zero, ridge regression doesn't penalize coefficients to exactly zero.

By placing a greater penalty on model complexity compared to standard ordinary least squares (OLS) regression, a subset of estimated coefficients in penalized regression become fixed at 0. This yields models that have better predictive accuracy than OLS estimates (Tibshirani, 1996). A challenge in implementing penalized regression techniques is that the regularization parameter λ needs to be chosen or estimated. Routines for comparing values of λ can be compared via cross-validation with bootstrapped datasets. Like stepwise or all subsets regression, these methods are available in several R packages; examples include 'lars' to implement least angle regression (Efron et al., 2004), 'elasticnet' to implement a hybrid L1/L2 penalization (Zou & Hastie, 2005), 'penalized' (Goeman, Meijer & Chaturvedi, 2018), and 'glmnet' (Friedman, Hastie & Tibshirani, 2010). Several applications of these methods exist in the context of VAR models (e.g. BigVAR, Nicholson, Matteson & Bien, 2019), though these have generally been developed in a maximum likelihood setting.

In addition to the maximum likelihood approaches, Bayesian lasso methods have been developed that treat the regularization parameter λ as an estimated hyper-parameter; by integrating over values of λ via Markov Chain Monte Carlo (MCMC), robust coefficient

estimates that are marginalized over values of λ can be generated (Kyung *et al.* 2010). Mechanistically, this involves specifying double-exponential or Laplace priors on regression coefficients (Park & Casella, 2008; O'Hara & Sillanpää, 2009). Alternative Bayesian priors to the lasso include mixture or "spike-slab" priors (Miller 2002; reviewed by O'Hara & Sillanpää 2009). Spike-slab priors on potentially sparse coefficients model the prior variance as a mixture of a wide distribution with high variance (the "slab") and a narrow distribution with small variance (the "spike" near zero). The contribution of each component can either be fixed a priori or estimated; challenges in implementing this type of shrinkage prior is that data-specific tuning is often required to ensure mixing between the two distributions, and results may be sensitive to the choice of tuning parameters (O'Hara & Sillanpää 2009). Because of computational challenges with the spike-slab, alternatives continuous priors such as the horseshoe prior have been a focus of recent development (Carvalho, Polson & Scott, 2010). Because of their flexibility and scalability (Piironen & Vehtari, 2017), these approaches have been incorporated into a number of software packages and are becoming widespread.

The objectives of our paper are to extend regularizing priors to Bayesian VAR models for ecological applications and develop software to implement these methods. We explore a range of potential priors for off-diagonal coefficients; examples include regularized normal and Student-t distributions, and a regularized horseshoe prior. The sensitivity of model estimates to the choice of prior is evaluated using simulated data for models with and without observation error. As a case study, we compare the performance of these Bayesian regularization techniques to a high dimensional VAR model explaining the dynamics of 37 marine species from the California Current in the North East Pacific

Ocean. All code for these models is deployed as a publicly available 'varlasso' R package, <https://github.com/atsa-es/varlasso> (Ward, Marshall & Scheuerell, 2022).

Methods

Vector autoregressive state space models

Vector autoregressive (VAR) models have been widely used in fisheries and related fields (these approaches are also known as multivariate autoregressive or MAR models). In the ecological literature, these are also referred to as the discrete time multivariate Gompertz models (Mutshinda, O'Hara & Woiwod, 2009). The VAR model consists of a process equation, $\mathbf{x}_{t+1} = \mathbf{B}\mathbf{x}_t + \mathbf{u} + \mathbf{w}_t$, where \mathbf{x}_t is an $m \times 1$ vector of log-abundances for species at time t , \mathbf{u} is an $m \times 1$ vector of species-specific growth rates or trends, \mathbf{B} represents a $m \times m$ matrix of community interactions (element $\mathbf{B}_{i,j}$ describes the per-capita effect of species j on species i), and \mathbf{w}_t represents an $m \times 1$ vector of random environmental effects at time t (Ives et al., 2003; Scheef et al., 2012). We assume environmental stochasticity is multivariate normal, such that $\mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{Q})$, and \mathbf{Q} may be a diagonal variance-covariance matrix (species have independent dynamics) or include correlation between species. The basic VAR model can be modified to also incorporate an observation error model (yielding a state-space, or VARSS model). The observation equation relates the true states of nature at time t (\mathbf{x}_t) to the observed data (\mathbf{y}_t), $\mathbf{y}_t = \mathbf{x}_t + \mathbf{v}_t$, where $\mathbf{v}_t \sim \text{MVN}(\mathbf{0}, \mathbf{R})$, and \mathbf{R} represents the variance-covariance matrix of observation errors (Holmes, Ward & Wills, 2012). In addition to partitioning the total variance into process and observation errors, the VARSS model is flexible in that it is better suited for datasets with lots of missing

values. In contrast, only abundance estimates that are adjacent in time contribute to the likelihood for the simpler VAR model (Ives et al., 2003).

Simulated data

We simulated datasets using estimated interactions from a simplified lake food web with 4 species groups described by (Ives et al., 2003). The interaction matrix for the low-planktivory system from Ives et al. (2003) is typical of many ecological applications in that (1) interspecific interactions (off-diagonal elements) are generally weaker than intraspecific interactions (density dependence, diagonal elements) and (2) a relatively large number of elements are 0 (8 of 16, Table S1).

We treated process errors as independent and identically distributed, such that $\mathbf{Q} = \sigma_{pro}^2 \mathbf{I}$, with σ_{pro} fixed at 0.2. For simulations focused on VAR models, observation error was not included. Observation error was added for VARSS simulations, with observation errors also assumed to be independent and identically distributed, such that, $\mathbf{R} = \sigma_{obs}^2 \mathbf{I}$. To explore several ratios of $\sigma_{obs}:\sigma_{proc}$, we varied σ_{obs} across three levels (0.05, 0.1, 0.2). For each combination of observation and process variance, we used 200 replicate datasets, each consisting of 40 timesteps. To ensure time series were approximately stationary, we performed a 'burn-in' of 200 timesteps for each, retaining the last 40 data points.


Priors

To compare the effects of regularizing priors, we applied three estimation models to each of our simulated datasets, varying only the prior formulations for the off-diagonal

elements of the \mathbf{B} matrix. Each estimation model assigned $B_{i,i} \sim \text{Normal}(0.7, 1)$ priors to diagonal elements of \mathbf{B} (representing intraspecific interactions) and truncated $\text{Normal}(0.0, 0.5)$ priors to the observation and process standard deviations ($\sigma_{obs}, \sigma_{pro}$). We assumed that both process and observation errors were uncorrelated across taxa, so that $\mathbf{Q} = \sigma_{pro}^2 \mathbf{I}$ and $\mathbf{R} = \sigma_{obs}^2 \mathbf{I}$.

Our three alternative formulations for priors on the off-diagonal elements of \mathbf{B} were:

(1) Normal distribution

We implemented normal priors on off-diagonal elements to represent the status quo for Bayesian VAR models (Mutshinda et al., 2019). In this approach, $B_{i,j} \sim \text{Normal}(0.0, \sigma_N)$ and σ_N is assumed known. light deviation from Normal priors is to use Student-t priors, which can generate similar distributions to the Normal with large degrees of freedom (ν), but also place more density on extreme values. In contrast to the unpooled approach where $B_{i,j}$ are estimated independently, a partial pooling approach may be used with either the Normal or Student-t distribution to shrink estimates toward a common mean (in this case, 0). Partial pooling can be implemented by assigning a hyper-prior to σ_N . We include support for the Student-t distribution and partial pooling in our `varlasso` R package, but they are not included in our simulation analyses.

(2) Laplace distribution

As a second prior, we used a Laplace or double exponential prior (O'Hara & Sillanpää, 2009; Casella et al., 2010) (Fig. 1). Relative to the Normal distribution, the Laplace can place greater density near 0, and is controlled by a single parameter that controls the

213 variance, $B_{i,j} \sim \text{Laplace}(0.0, \tau)$. An equivalent parameterization is as a mixture, $\alpha \sim \text{Exp}\left(\frac{1}{2\tau^2}\right)$
 214 where $B_{i,j} \sim \text{Normal}(0.0, \sqrt{\alpha})$ (Ding & Blitzstein, 2018).
 215 (3) Regularized horseshoe prior
 216 As our third prior, we implement regularized horseshoe priors (Piironen & Vehtari, 2017)
 217 (Fig. 1). We use the same implementation as rstanarm and brms (Bürkner, 2017; Goodrich
 218 et al., 2020), so that priors on off-diagonal elements of \mathbf{B} are $B_{i,j} \sim \text{Normal}(0.0, \tau^2 \tilde{\lambda}_{i,j}^2)$. The
 219 hyperparameter τ is assigned a $\tau \sim \text{Student} - t(v = 3, 0, \phi)$ where ϕ is a global scale
 220 parameter and $\tilde{\lambda}_{i,j}^2$ controls the regularization for the effect of species j on species i in the \mathbf{B}
 221 matrix. The degree of regularization is allowed to be unique by modeling it as $\tilde{\lambda}_{i,j}^2 = \frac{c^2 \lambda_{i,j}^2}{c^2 + \tau^2 \lambda_{i,j}^2}$,
 222 and $\lambda_{i,j}^2$ are treated as parameters with priors $\lambda_{i,j}^2 \sim \text{Cauchy}(0, 1)$. The width of the slab
 223 (allowing for large \mathbf{B} coefficients) is assigned a prior $c^2 \sim \text{InvGamma}\left(\alpha = \frac{v_{slab}}{2}, \beta = \frac{s_{slab}^2 v_{slab}}{2}\right)$,
 224 where v_{slab} is the degrees of freedom and s_{slab}^2 is the scale of the slab.

225

226 *Hyperparameters*

227 We carefully selected hyperparameters for each of the three prior formulations, to
 228 ensure that the priors would have the same target standard deviation. Starting with the
 229 regularized horseshoe prior, we followed the advice of (Piironen & Vehtari, 2017), and we
 230 held the global $df = 1$. The same authors recommend quantifying ϕ (the global scale
 231 hyperparameter) as the ratio of non-zero coefficients to coefficients that are zero to the
 232 square root of the number of observations. Because of the multivariate nature of a VAR
 233 model, we constructed several preliminary scenarios letting the global scale range from


0.025 to 0.08 and found that $\phi=0.025$ resulted in reasonable performance. We also used these preliminary model runs to consider several combinations of slab parameters; based on these simulations, we used $v_{slab}=5$ and $s_{slab}^2=1.0$. Combined, these choices of hyperparameters resulted in a prior with a standard deviation ~ 0.24 ; as a result we used values of $v_{LP} = 3$ and $\phi_{LP} = 0.165$ for the Laplace prior, and fixed $\sigma_N = 0.24$ for the Normal prior.

Estimation

Estimation was done in a Bayesian framework using our varlasso R package (Ward, Marshall & Scheuerell, 2022). This package is built in R (R Core Team, 2021) and acts as an interface to Stan (Stan Development Team, 2022), which implements ~~Markov chain Monte Carlo (MCMC)~~ using the No-U Turn Sampling (NUTS) algorithm (Hoffman & Gelman, 2014; Carpenter et al., 2017). For all models, we ran 3 parallel MCMC chains, discarding the first 2000 iterations of each and retaining the last 1000 samples. In addition to using visual diagnostics (Gabry, 2018), we calculated R-hat statistics to evaluate convergence (Vehtari et al., 2021).

Quantifying performance

We used two metrics to quantify the performance of alternative model formulations, as there may be multiple objectives of VARSS analyses. To compare the influence of priors on overall predictive ability, we calculated the approximate Leave-One-Out Information Criterion (LOOIC) in the 'loo' R package (Vehtari, Gelman & Gabry, 2017; Vehtari et al., 2020). As a second metric, we computed log-score statistics to quantify the prior influence

on **B** matrix parameter estimates. Log-scores are often used to quantify the bias and precision of predictions (Gneiting & Raftery, 2007); similarly, they can also be used to quantify the predictions of parameter estimates when true values are known, as in the case of our simulations. The log-score can be calculated a number of ways, but involves evaluating an observation (or parameter value) y across a predictive density $f(y, \theta_{post}) = \frac{1}{n} \sum_{i=1:n} f(y | \theta_{i,post})$ where θ_{post} is a vector containing samples from the posterior. If the density $f()$ does not have a closed form, an alternative approach is to estimate the empirical CDF to approximate $f()$ (Krüger et al., 2021). We adopted this empirical approach, using the 'scoringRules' R package (Jordan, Krüger & Lerch, 2019) and calculated log-scores, $\log(f(\theta_{true}, \theta_{post}))$. 

Application to marine food webs

To demonstrate the utility of Bayesian regularization, we applied the approach described above to a VAR model describing the ecosystem dynamics of the California Current (Horne et al., 2010; Kaplan et al., 2013). The 'Atlantis' ecosystem modeling framework (Fulton et al., 2004) couples output from a hydrodynamic Regional Ocean Modeling System (ROMS) model with a spatially explicit food web model that may include 60+ functional groups, and includes fishing mortality. We used an Atlantis model implemented to represent the California Current marine ecosystem, including the fisheries it supports (Hermann et al., 2009; Horne et al., 2010; Kaplan et al., 2013; Marshall, Kaplan & Levin, 2014). Estimates of fish biomass for the California Current Atlantis Model are derived from fisheries stock assessments, survey indices, and published data on growth, life history, and food habits (Horne et al., 2010; Kaplan, Horne & Levin, 2012). We used the

baseline model configuration from Marshall et al. (2014) to generate ecosystem dynamics over a 50-year horizon. While Atlantis operates on a 12-hour time step, we used output at an annual time step to fit the VAR model. We restricted the analysis to the most recent 25 years of biomass to allow the model to reach quasi-equilibrium. We also restricted the time series to 37 (of 62) functional groups. Initial exploration revealed that the VAR models struggled to converge for functional groups with drastically different generation times (e.g., whales and zooplankton). Therefore, we focused on lower trophic level functional groups, in this case, prey and prey of prey of the mackerel functional group (including Pacific mackerel *Scomber japonicus* and jack mackerel *Trachurus symmetricus*). These modeled biomass time series were then used as responses in a VAR model of the California Current ecosystem (as observation error is not included as part of the Atlantis ecosystem model, we did not apply VARSS models to these data). Combined, these cutoffs yielded 925 data points; fitting this kind of data in a VAR framework where all interactions are possible (e.g. none are fixed *a priori* at 0) includes 1406 parameters (1369 interactions in **B**, 37 variance parameters in **Q**).

Instead of just focusing on changes in single interspecific interactions, a broader question of interest is whether ecological communities are stable. To illustrate the impact of regularization on inference about community stability, we used the posterior estimates of **B** to calculate two metrics proposed by (Ives et al., 2003). First we calculated the proportion of stationary variance attributed to species interactions, $\det|\mathbf{B}|^{2/m}$, where m is the number of species in the community. Values of this stability metric greater than 1 indicate unstable systems, and smaller values closer to 0 represent greater stability. Second, we calculated the rate of return, as the dominant eigenvalue of **B**. We calculated

each of the stability metrics separately for each MCMC draw to produce a posterior distribution of stability for each alternative prior formulation.

Results

Simulated data

Our comparison of priors (Normal, Laplace, Regularized horseshoe) to simulated data indicated that posterior distributions of **B** matrix parameters were qualitatively similar between the Laplace and horseshoe priors, with the latter assigning slightly more density near 0 (Fig. S1). The total log-score across all parameters in the **B** matrix indicated that the horseshoe prior generated estimates that were most accurate and precise (Fig. 2). Some modeling applications may be more or less concerned with estimates of density dependence (diagonal of **B**), or estimates of species interactions (off-diagonal elements of **B**). In our simulations, we found that the effect of priors was largest between estimates of off-diagonal elements of **B** (Fig. 2). Because of wider tails, the normal prior was better able to capture non-zero elements, but also worse at estimating elements of **B** that were assigned values of 0 (Fig. 2). When standardized to a common scale, the regularized priors do a better job at estimating non-zero elements than the normal prior does at estimating true zeros (Fig. 2). Our LOOIC comparison to quantify the impact of alternative priors on predictive accuracy showed that the Laplace and horseshoe priors were slightly better than the normal distribution (though these estimates have considerable uncertainty; Fig. S2).

Our simulations used a fixed process variance, and varied the level of observation error variance to explore how signal to noise ratios impact estimates of the **B** matrix elements. Varying the observation error highlighted that reducing observation error

326 minimizes the differences between priors (or in contrast, increasing observation error
327 makes the least accurate or precise priors even worse).

328 *Application to marine food webs*

329 In our application to data from the California Current marine food web of 37 marine
330 species, there were substantial differences in LOOIC between models with alternative
331 priors; the model with Gaussian priors had the highest estimate ($\text{LOOIC} = 389.3 \pm 45.6$),
332 followed by the Laplace prior (222.2 ± 69.4) and finally the model with regularized
333 horseshoe priors (-14.2 ± 65.7). These results indicate that the model with regularized
334 horseshoe priors (lowest LOOIC) has the best approximated out of sample predictive
335 ability.

336 The effects of regularized **B** matrix priors are easily seen when comparing estimates
337 from a VAR model with normal priors to one with regularized horseshoe priors (Fig. 3).
338 With regularization, the majority of off-diagonal **B** matrix elements are assigned values
339 close to 0. Despite zeroing out the majority of species interactions, the VAR model with
340 regularized horseshoe priors appears to identify ecologically important interactions. The
341 37 components of the food web in our analysis were centered around Pacific mackerel –
342 the interspecific effect that was found to have the largest estimated effect on mackerel
343 biomass is a positive effect of copepods (Fig. 4), an important diet items for this species
344 (Dufault, Marshall & Kaplan, 2009; Brodeur et al., 2019).

345 Finally, we compared the posterior distributions of estimated stability across
346 alternative prior formulations. These results indicated that there were slight increases in
347 estimated rates of return moving from horseshoe to Laplace to normal priors (Fig. 5).
348 Rates of return within the unit circle are expected in stationary systems (Ives et al. 2003),

and the model with the regularized horseshoe prior appears closest to this assumption. Stability, calculated as $\det|\mathbf{B}|^{2/37}$ was more similar across alternative prior formulations, with wide and overlapping credible intervals – though the point estimate for the model with horseshoe priors appeared slightly higher, translating to less stability (Fig. 5).

Discussion



As ecological datasets have grown larger and larger, statistical variable selection techniques have also evolved to reduce model complexity and help to identify important covariates. Penalized regression techniques offer several advantages over methods that are currently widely used in ecology (e.g., stepwise and all subsets regression). Regularizing priors, such as the Laplace and horseshoe used here offer several advantages over traditional methods. First, by including hyperparameters, uncertainty in the degree of regularization is propagated into the coefficient estimates. Second, model complexity is implicitly accounted for by setting many of the model coefficients near 0. Unlike stepwise variable selection, which may become trapped in valleys and need to be initialized from multiple starting points, a third advantage is that in the Bayesian approach, a model only needs to be run once (provided MCMC chains indicate convergence).



Results from our simulated datasets using regularizing priors and VAR models illustrated that because the Laplace or horseshoe priors will result in many posterior estimates near zero, models with those priors are better able to identify true zeros. As expected, advantages of regularizing priors generally diminish as observation error is increased and the signal to noise ratio is decreased (Fig. 2). Depending on whether these small interactions are a focus of inference, or whether the goal of an analysis is to find the VAR or VARSS model with the best predictive ability, the Laplace or regularizing horseshoe

may each offer advantages. While we used log-scores to quantify the accuracy and precision of alternative models, other studies may be interested in other types of predictive performance (e.g. out of sample forecasting) and results would be expected to differ slightly depending on the type of inference. Regardless of the application, we recommend analysts compare the results from several formulations of priors, after establishing the goals of the modeling.

Our estimation of interactions among 37 species in the California Current ecosystem represents a more realistic ecological analysis, where the potential complexity of the model exceeds the number of data points. With regularizing priors, posterior estimates of interspecific interactions from the Bayesian VAR model were generally shrunk toward zero (representing weak interactions, Fig. 3). As this food web was constructed with mackerel as a central focus, it is promising that the strongest interspecific effects on mackerel is a positive effect of copepods. Large zooplankton (euphausiids) are the most important diet item for mackerel in the California Current Atlantis model, however the strength of the copepod result may be driven by both direct and indirect interactions (copepods are a diet item for mackerel, but also are the primary prey of euphausiids). A similar strong linkage between mackerel and copepods was also found in Kaplan et al. (2014) – they simulated the effects of various levels of fishing pressure on forage fishes and found that scenarios with high exploitation rates of mackerel had a positive effect on euphausiids, and subsequent negative interactions on copepods.

Ecological applications of multi-species models are increasingly common (Hampton *et al.* 2013a). For example, they have been used to examine food web dynamics in plankton communities (Ives *et al.* 2003; Hampton, Scheuerell & Schindler 2006), analyze effects of

shifting climate on large ecosystems (Hampton *et al.* 2008; Francis *et al.* 2012), illustrate portfolio effects in coral fishes (Thibaut, Connolly & Sweatman 2012), and evaluate varying effects of commercial fisheries (Dalton 2001; Lindegren *et al.* 2009). Combining regularizing priors with VAR or VARSS time series models offers one approach to simplifying the complexity of a large food web into a smaller number of interpretable components and indicators of emergent properties like stability. Future advances with these models could experiment with the inclusion of sample replicates, known observation errors (via other surveys for example), and time-varying interactions.

Acknowledgements

The authors would like to thank M. Betancourt and J. Arnold for developing clear vignettes and case studies with guidelines around Bayesian regularization. KM was supported on a National Research Council (NRC) post-doctoral fellowship at the Northwest Fisheries Science Center while this research was performed. I. Kaplan for providing helpful edits and discussions about the Atlantis model, as well as to B. Fulton for Atlantis model development. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Anderson DR, Burnham KP, Gould WR, Cherry S. 2001. Concerns about finding effects that are actually spurious. *Wildlife Society Bulletin (1973-2006)* 29:311–316.
- Bartoń K. 2020. *MuMIn: Multi-Model Inference*.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135. DOI: 10.1016/j.tree.2008.10.008.
- Brodeur RD, Hunsicker ME, Hann A, Miller TW. 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. *Marine Ecology Progress Series* 617–618:149–163. DOI: 10.3354/meps12497.
- Bürkner P-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80:1–28. DOI: 10.18637/jss.v080.i01.
- Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A. 2017. Stan: A probabilistic programming language. *Journal of statistical software* 76.
- Carvalho CM, Polson NG, Scott JG. 2010. The horseshoe estimator for sparse signals. *Biometrika* 97:465–480. DOI: 10.1093/biomet/asq017.
- Casella G, Ghosh M, Gill J, Kyung M. 2010. Penalized regression, standard errors, and Bayesian lassos. *Bayesian Analysis* 5:369–411. DOI: 10.1214/10-BA607.
- Crowder L, Norse E. 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy* 32:772–778. DOI: 10.1016/j.marpol.2008.03.012.

435 Ding P, Blitzstein JK. 2018. On the Gaussian mixture representation of the Laplace
436 distribution. *The American Statistician* 72:172–174. DOI:
437 10.1080/00031305.2017.1291448.

438 Dufault AM, Marshall KN, Kaplan IC. 2009. A synthesis of diets and trophic overlap of
439 marine species in the California Current. NOAA Technical Memorandum NMFS-
440 NWFSC-103, Seattle, WA: U.S. Dept. Commer.

441 Efron B, Hastie T, Johnstone I, Tibshirani R. 2004. Least angle regression. *The Annals of*
442 *Statistics* 32:407–499. DOI: 10.1214/009053604000000067.

443 Friedman J, Hastie T, Tibshirani R. 2010. Regularization paths for generalized linear models
444 via coordinate descent. *Journal of Statistical Software* 33:1–22.

445 Fulton EA, Parslow JS, Smith ADM, Johnson CR. 2004. Biogeochemical marine ecosystem
446 models II: the effect of physiological detail on model performance. *Ecological*
447 *Modelling* 173:371–406. DOI: 10.1016/j.ecolmodel.2003.09.024.

448 Fulton EA, Smith ADM, Johnson CR. 2003. Effect of complexity on marine ecosystem
449 models. *Marine Ecology Progress Series* 253:1–16. DOI: 10.3354/meps253001.

450 Gabry J. 2018. *shinystan: Interactive Visual and Numerical Diagnostics and Posterior Analysis*
451 *for Bayesian Models*.

452 Gneiting T, Raftery AE. 2007. Strictly proper scoring rules, prediction, and estimation.
453 *Journal of the American Statistical Association* 102:359–378. DOI:
454 10.1198/016214506000001437.

455 Goeman JJ, Meijer RJ, Chaturvedi N. 2018. *penalized: L1 (lasso and fused lasso) and L2*
456 *(ridge) penalized estimation in GLMs and in the Cox model*.

457 Goodrich B, Gabry J, Ali I, Brilleman S. 2020. *rstanarm: Bayesian applied regression modeling*
458 *via Stan*.

459 Hampton SE, Holmes EE, Scheef LP, Scheuerell MD, Katz SL, Pendleton DE, Ward EJ. 2013a.
460 Quantifying effects of abiotic and biotic drivers on community dynamics with
461 multivariate autoregressive (MAR) models. *Ecology* 94:2663–2669. DOI:
462 10.1890/13-0996.1.

463 Hampton SE, Strasser CA, Tewksbury JJ, Gram WK, Budden AE, Batcheller AL, Duke CS,
464 Porter JH. 2013b. Big data and the future of ecology. *Frontiers in Ecology and the*
465 *Environment* 11:156–162. DOI: 10.1890/120103.

466 Harvey C, Garfield N, Williams G, Tolimieri N, Schroeder I, Hazen E, Andrews K, Barnas K,
467 Bograd S, Brodeur R, Burke B, Cope J, deWitt L. 2018. *Ecosystem Status Report of the*
468 *California Current for 2018: A Summary of Ecosystem Indicators Compiled by the*
469 *California Current Integrated Ecosystem Assessment Team (CCIEA)*. U.S.
470 DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration
471 National Marine Fisheries Service Northwest Fisheries Science Center.

472 Hermann AJ, Curchitser EN, Haidvogel DB, Dobbins EL. 2009. A comparison of remote vs.
473 local influence of El Niño on the coastal circulation of the northeast Pacific. *Deep Sea*
474 *Research Part II: Topical Studies in Oceanography* 56:2427–2443. DOI:
475 10.1016/j.dsr2.2009.02.005.

476 Hocking RR. 1976. A Biometrics Invited Paper. The analysis and selection of variables in
477 linear regression. *Biometrics* 32:1–49. DOI: 10.2307/2529336.

478 Hoerl AE, Kennard RW. 1970. Ridge regression: biased estimation for nonorthogonal
479 problems. *Technometrics* 42:80–86. DOI: 10.2307/1271436.

480 Hoffman MD, Gelman A. 2014. The No-U-turn sampler: adaptively setting path lengths in
481 Hamiltonian Monte Carlo. *The Journal of Machine Learning Research* 15:1593–1623.

482 Holmes EE, Ward EJ, Wills K. 2012. MARSS: Multivariate autoregressive state-space models
483 for analyzing time-series data. *The R Journal* 4:11–19.

484 Horne PJ, Kaplan IC, Marshall KN, Levin PS, Harvey CJ, Hermann AJ, Fulton EA. 2010. *Design
485 and parameterization of a spatially explicit ecosystem model of the central California
486 Current*. Seattle, WA: Northwest Fisheries Science Center, National Marine Fisheries
487 Service, National Oceanic and Atmospheric Administration.

488 Howe D, Costanzo M, Fey P, Gojobori T, Hannick L, Hide W, Hill DP, Kania R, Schaeffer M, St
489 Pierre S, Twigger S, White O, Yon Rhee S. 2008. The future of biocuration. *Nature*
490 455:47–50. DOI: 10.1038/455047a.

491 Ives AR, Dennis B, Cottingham KL, Carpenter SR. 2003. Estimating community stability and
492 ecological interactions from time-series data. *Ecological Monographs* 73:301–330.
493 DOI: 10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2.

494 Jordan A, Krüger F, Lerch S. 2019. Evaluating probabilistic forecasts with scoringRules.
495 *Journal of Statistical Software* 90:1–37. DOI: 10.18637/jss.v090.i12.

496 Kaplan IC, Brown CJ, Fulton EA, Gray IA, Field JC, Smith ADM. 2013. Impacts of depleting
497 forage species in the California Current. *Environmental Conservation* 40:380–393.
498 DOI: 10.1017/S0376892913000052.

499 Kaplan IC, Horne PJ, Levin PS. 2012. Screening California Current fishery management
500 scenarios using the Atlantis end-to-end ecosystem model. *Progress in Oceanography*
501 102:5–18. DOI: 10.1016/j.pocean.2012.03.009.

502 Krüger F, Lerch S, Thorarinsdottir T, Gneiting T. 2021. Predictive inference based on
503 Markov Chain Monte Carlo Output. *International Statistical Review* 89:274–301. DOI:
504 10.1111/insr.12405.

505 Marshall KN, Kaplan IC, Levin PS. 2014. New target fisheries lead to spatially variable food
506 web effects in an ecosystem model of the California Current. *Ecological Modelling*
507 289:96–105. DOI: 10.1016/j.ecolmodel.2014.07.003.

508 Miller AJ. 2002. *Subset selection in regression*. Boca Raton, Florida: Chapman & Hall / CRC.

509 Miller TL based on F code by A. 2020. *leaps: Regression Subset Selection*.

510 Mundry R, Nunn CL. 2009. Stepwise model fitting and statistical inference: turning noise
511 into signal pollution. *The American Naturalist* 173:119–123. DOI: 10.1086/593303.

512 Mutshinda CM, Finkel ZV, Widdicombe CE, Irwin AJ. 2019. Bayesian inference to partition
513 determinants of community dynamics from observational time series. *Community*
514 *Ecology* 20:238–251. DOI: 10.1556/168.2019.20.3.4.

515 Mutshinda CM, O’Hara RB, Woiwod IP. 2009. What drives community dynamics?
516 *Proceedings of the Royal Society B: Biological Sciences* 276:2923–2929. DOI:
517 10.1098/rspb.2009.0523.

518 Nicholson W, Matteson D, Bien J. 2019. *BigVAR: Dimension Reduction Methods for*
519 *Multivariate Time Series*.

520 O’Hara RB, Sillanpää MJ. 2009. A review of Bayesian variable selection methods: what, how
521 and which. *Bayesian Analysis* 4:85–117. DOI: 10.1214/09-BA403.

522 Olden JD, Jackson DA. 2000. Torturing data for the sake of generality: How valid are our
523 regression models? *Écoscience* 7:501–510. DOI:
524 10.1080/11956860.2000.11682622.

525 Ovaskainen O, Tikhonov G, Dunson D, Grøtan V, Engen S, Sæther B-E, Abrego N. 2017. How
526 are species interactions structured in species-rich communities? A new method for
527 analysing time-series data. *Proceedings of the Royal Society B: Biological Sciences*
528 284:20170768. DOI: 10.1098/rspb.2017.0768.

529 Park T, Casella G. 2008. The Bayesian Lasso. *Journal of the American Statistical Association*
530 103:681–686. DOI: 10.1198/016214508000000337.

531 Piironen J, Vehtari A. 2017. Sparsity information and regularization in the horseshoe and
532 other shrinkage priors. *Electronic Journal of Statistics* 11:5018–5051. DOI:
533 10.1214/17-EJS1337SI.

534 R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna,
535 Austria: R Foundation for Statistical Computing.

536 Scheef LP, Pendleton DE, Hampton SE, Katz SL, Holmes EE, Scheuerell MD, Johns DG. 2012.
537 Assessing marine plankton community structure from long-term monitoring data
538 with multivariate autoregressive (MAR) models: a comparison of fixed station
539 versus spatially distributed sampling data. *Limnology and Oceanography: Methods*
540 10:54–64. DOI: 10.4319/lom.2012.10.54.

541 Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W,
542 Sykes MT, Thonicke K, Venevsky S. 2003. Evaluation of ecosystem dynamics, plant
543 geography and terrestrial carbon cycling in the LPJ dynamic global vegetation
544 model. *Global Change Biology* 9:161–185. DOI: 10.1046/j.1365-2486.2003.00569.x.

545 Spiegelhalter DJ, Best NG, Carlin BP, Van Der Linde A. 2002. Bayesian measures of model
546 complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical*
547 *Methodology)* 64:583–639. DOI: 10.1111/1467-9868.00353.

548 Stan Development Team. 2022. *Stan Modeling Language Users Guide and Reference Manual*,
549 v.2.28 <https://mc-stan.org>.

550 Tibshirani R. 1996. Regression shrinkage and selection via the lasso. *Journal of the Royal*
551 *Statistical Society. Series B (Methodological)* 58:267–288.

552 Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner P-C, Paananen T, Gelman A. 2020. loo:
553 Efficient leave-one-out cross-validation and WAIC for Bayesian models.

554 Vehtari A, Gelman A, Gabry J. 2017. Practical Bayesian model evaluation using leave-one-
555 out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432. DOI:
556 10.1007/s11222-016-9696-4.

557 Vehtari A, Gelman A, Simpson D, Carpenter B, Bürkner P-C. 2021. Rank-normalization,
558 folding, and localization: An improved Rhat for assessing convergence of MCMC
559 (with discussion). *Bayesian Analysis*.

560 Venables WN, Ripley BD. 2002. *Modern Applied Statistics with S*. New York: Springer.

561 Ward EJ, Marshall KN, Scheuerell MD. 2022. *varlasso: An R Package for Regularized*
562 *Bayesian VAR and VARSS models*. Zenodo. DOI: 10.5281/zenodo.5879725.

563 West M. 2003. Bayesian Factor Regression Models in the “Large p, Small n” Paradigm. In:
564 *Bayesian Statistics*. Oxford University Press, 723–732.

565 Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP. 2006. Why do we still use
566 stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75:1182–
567 1189. DOI: 10.1111/j.1365-2656.2006.01141.x.

568 Wu TT, Lange K. 2008. Coordinate descent algorithms for lasso penalized regression. *The*
569 *Annals of Applied Statistics* 2:224–244. DOI: 10.1214/07-AOAS147.

570 Zar JH. 1999. *Biostatistical Analysis*. New Jersey: Simon and Schuster.

Zou H, Hastie T. 2005. Regularization and variable selection via the elastic net. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 67:301–320. DOI: 10.1111/j.1467-9868.2005.00503.x.

Figure Legends

Figure 1. Illustration of 3 potential prior distributions for interactions in VAR and VARSS models. All three priors are centered on 0 and their standard deviations are equal ($\sigma \sim 0.24$).

Figure 2. Distribution of the average difference in log-scores between alternative priors on **B** matrix elements and the best model (each box represents 200 replicated datasets, and with values of 0 representing the best model). Values are averaged to allow comparison between (1) all **B** parameters, (2) diagonal elements, (3) off-diagonal elements that are not zero, and (4) off-diagonal elements that are zero.

Figure 3. Posterior means of species interaction estimates from the **B** matrix for the California Current marine food web. Results from using two priors for the off-diagonal elements are shown: a normal prior with each element estimated as a unique parameter, and a regularized horseshoe prior. Diagonal elements generally have a different range (0 – 1) compared to off-diagonal elements. Figure 4. Time series of standardized biomass for mackerel and copepods, used in the VAR model of the California Current marine community. The two strongest effects on mackerel biomass are also shown (positive effect of copepods on mackerel, and a slight degree of density dependence of mackerel).

594 Figure 5. Posterior distributions of community stability from the VAR models of the
 595 California Current marine food web, derived as $\det(\mathbf{B})^{2/37}$ and the dominant eigenvalue of
 596 \mathbf{B} . Estimates are shown across a range of potential priors for the off-diagonal elements of \mathbf{B} .
 597 Boxes represent the posterior quartiles (and median) and the vertical lines represent the
 598 upper and lower extremes.

Figure 1

Figure 1

Illustration of 3 potential prior distributions for interactions in VAR and VARSS models. All three priors are centered on 0 and their standard deviations are equal (0.24)

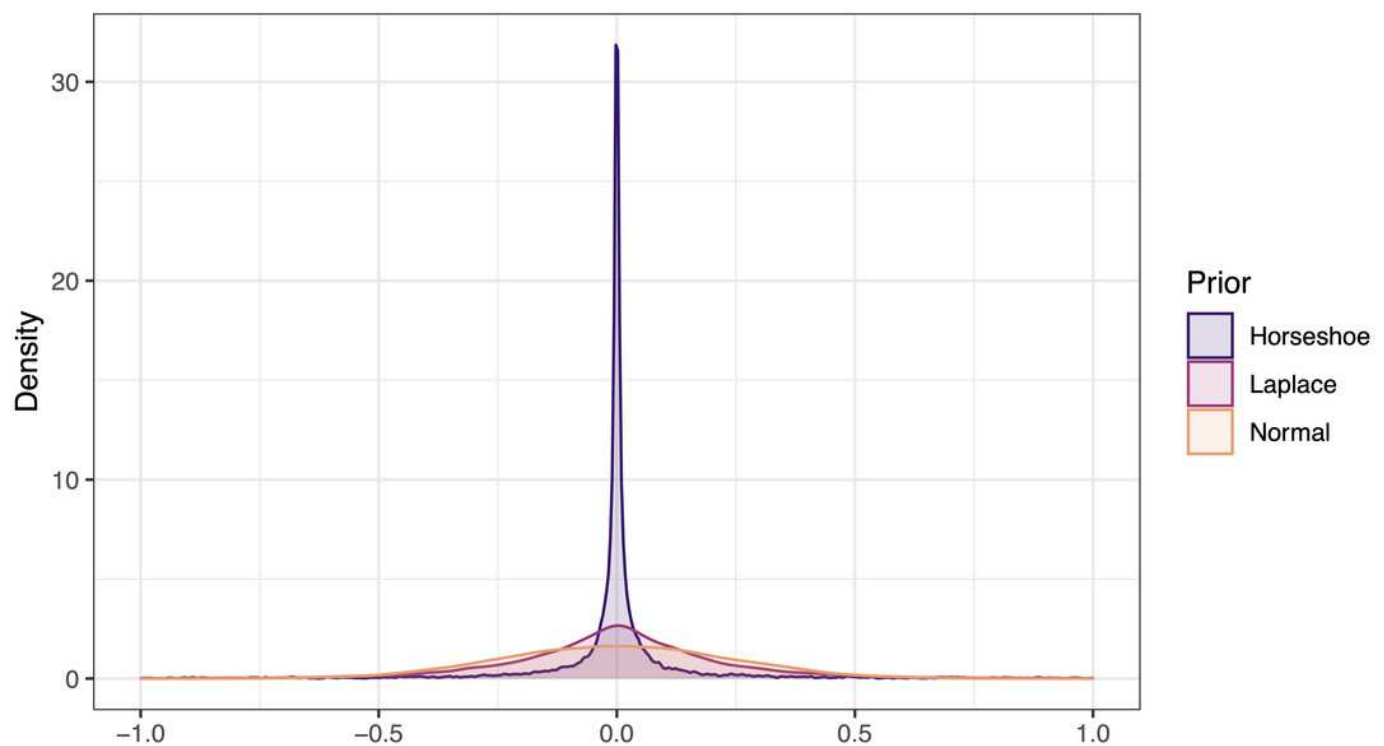


Figure 2

Figure 2

Distribution of the average difference in log-scores between alternative priors on **B** matrix elements and the best model (each box represents 200 replicated datasets, and with values of 0 representing the best model). Values are averaged to allow comparison between (1) all **B** parameters, (2) diagonal elements, (3) off-diagonal elements that are not zero, and (4) off-diagonal elements that are zero

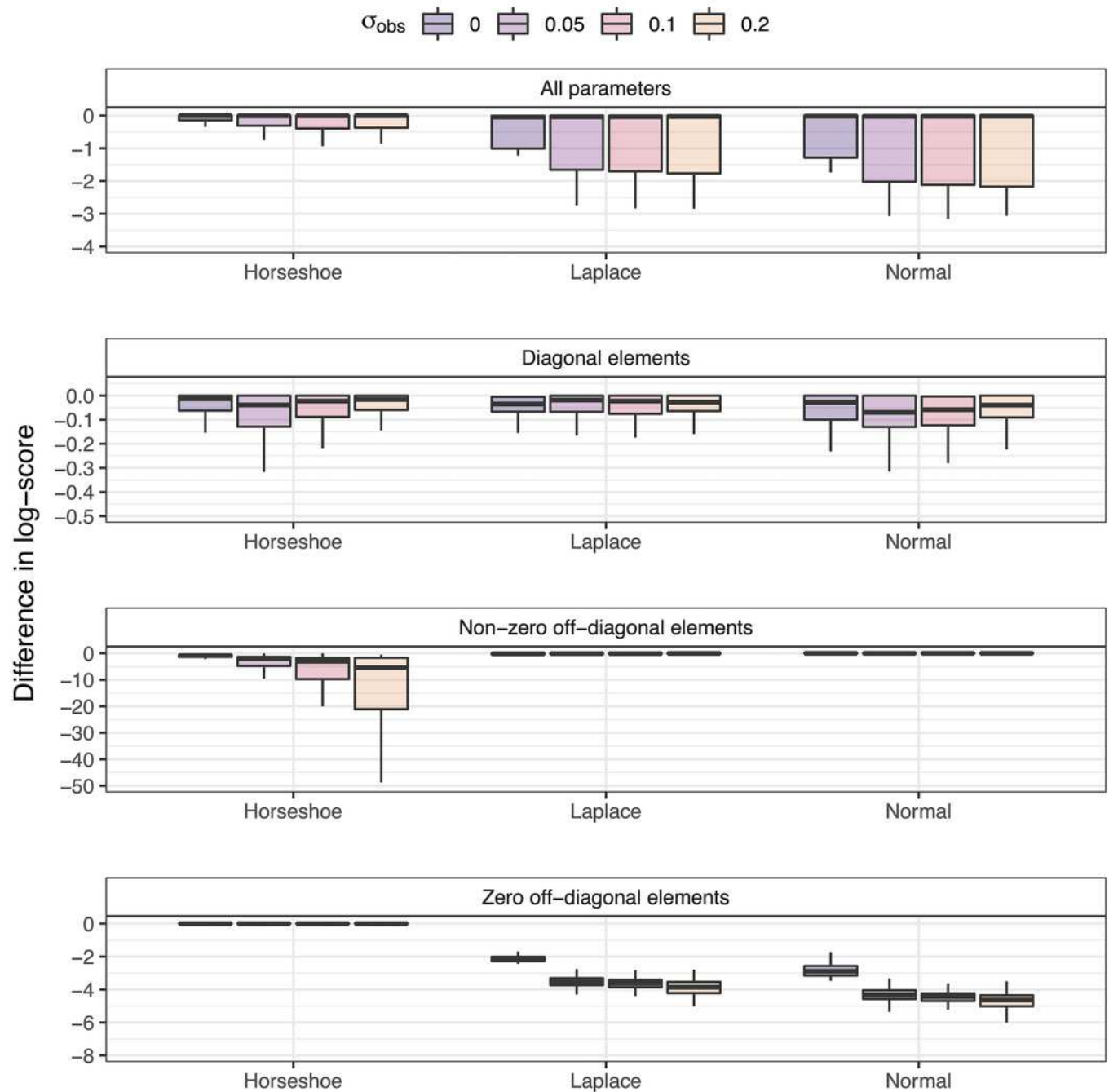


Figure 3

Figure 3

Posterior means of species interaction estimates from the **B** matrix for the California Current marine food web. Results from using two priors for the off-diagonal elements are shown: a normal prior with each element estimated as a unique parameter, and a regularized horseshoe prior. Diagonal elements generally have a different range (0 – 1) compared to off-diagonal elements.

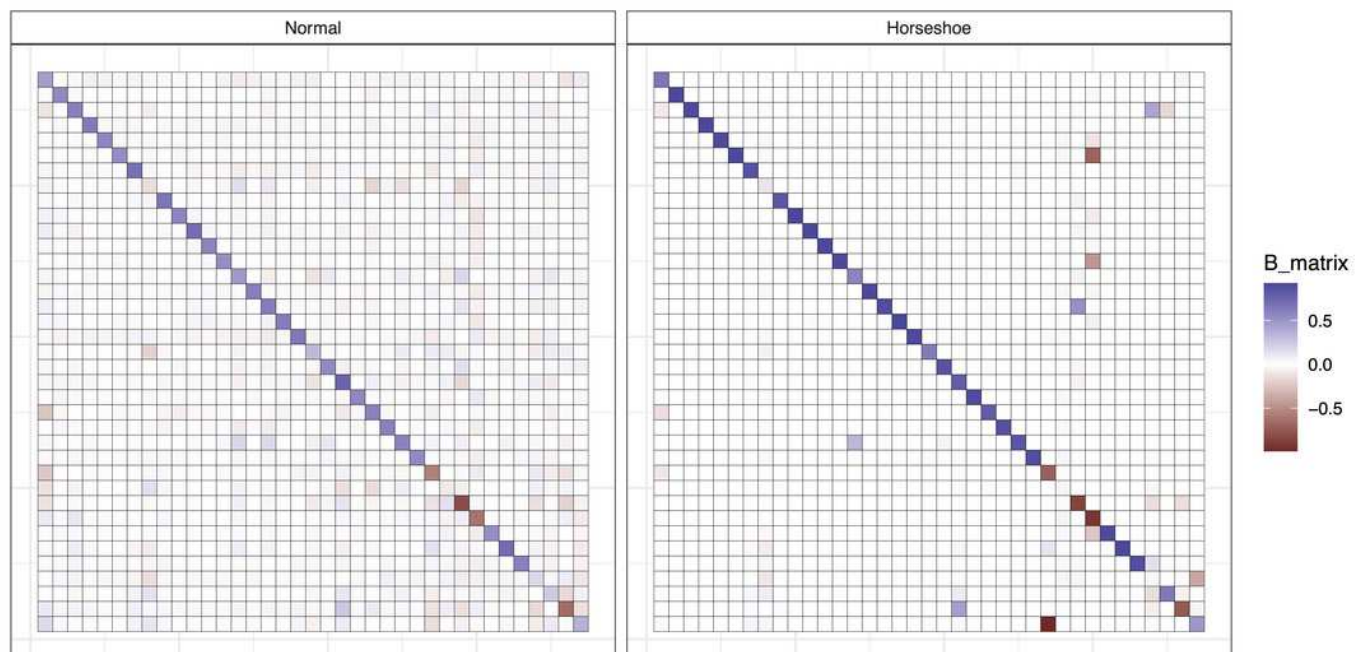


Figure 4

Figure 4

Time series of standardized biomass for mackerel and copepods, used in the VAR model of the California Current marine community. The two strongest effects on mackerel biomass are also shown (positive effect of copepods on mackerel, and a slight degree of density dependence of mackerel).

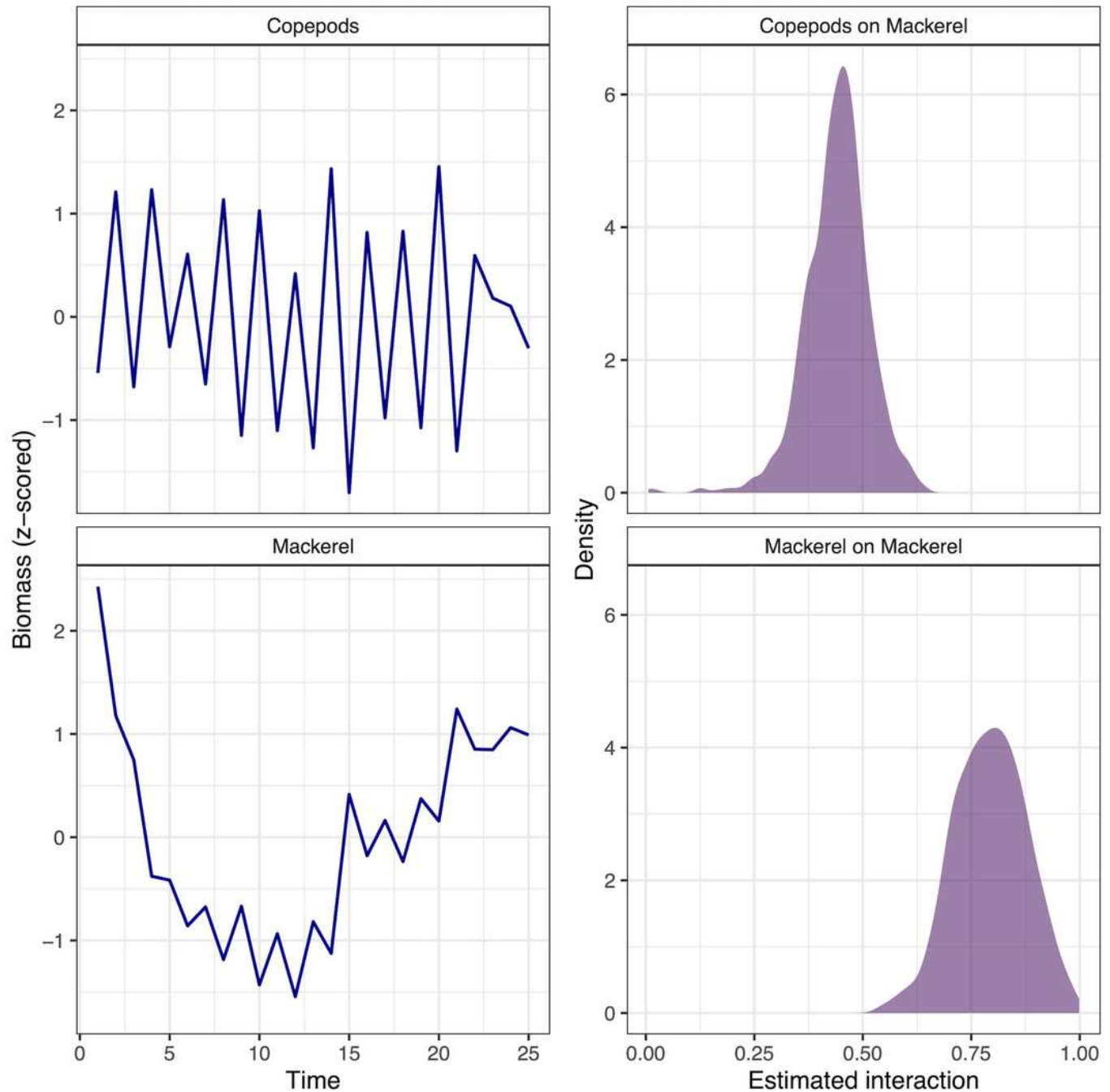


Figure 5

Figure 5

Posterior distributions of community stability from the VAR models of the California Current marine food web, derived as $\det(B)^{(2/37)}$ and the dominant eigenvalue of B. Estimates are shown across a range of potential priors for the off-diagonal elements of B. Boxes represent the posterior quartiles (and median) and the vertical lines represent the upper and lower extremes.

